

# Glossary

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**adaptation** A trait that enhances fitness (survivorship and reproduction). Also, an evolutionary process that results in a population of individuals with traits best suited to the current environment.

**additive effects (A)** The average effect of individual alleles on the phenotype.

**aggressive mimicry** A situation in which a predator mimics a nonthreatening model.

**alarm call** A unique vocalization produced by social animals when a predator is nearby.

**alarm signal hypothesis** The hypothesis that advertisement behavior functions to warn nearby conspecifics of danger.

**Allee effect** A situation in which the fitness of individuals increases with increased population density.

**allogrooming** The grooming by one individual of another to remove ectoparasites.

**alternate hypothesis ( $H_a$ )** The statistical hypothesis that the proposed explanation for an observation does significantly affect the behavior of the organism.

**alternative reproductive tactics** The existence of multiple behavioral mating phenotypes in a population.

**altruism** A behavior that results in the increased fitness of another individual and involves a cost to the individual performing the behavior. Also known as helping behavior.

**ancestral trait** A trait found in the common ancestor of two or more species. Also called a **plesiomorphic trait**.

**animal behavior** Any internally coordinated, externally visible pattern of activity that responds to changing external or internal conditions.

**animal culture** Differences in multiple traditions among populations.

**anisogamy** The existence of differently sized gametes (small and large) in the different sexes.

**anthropomorphism** The attribution of human motivations, characteristics, or emotions to animals.

**apomorphic trait** A trait found in an organism that was not present in the last common ancestor of a group of two or more species. Also known as a **derived trait**.

**aposematic coloration** Brightly colored morphology in a species that stands out from the environment and is associated with noxious chemicals or poisons that make individuals unpalatable or dangerous prey.

**audience effect** The presence of a bystander influences the behavior of a signaler.

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**bar graph** A graph that represents categorical data in rectangular bars arranged horizontally or vertically.

**Bateman's hypothesis** The hypothesis that female reproductive success is most strongly limited by the number and success of eggs that a female can produce, while male reproductive success is limited by the number of mates a male has.

**Batesian mimicry** The resemblance of a palatable mimic to an unpalatable model that predators have learned to avoid.

**behavioral traditions** Differences in behavior among populations that are transmitted between generations through social learning.

**bicoordinate navigation** The ability to identify a geographic location using two varying environmental gradients.

**biparental care** Both parents provide care for offspring.

**breeding dispersal** The abandonment of one breeding site to move to another.

**brood parasitism** A behavior in which a female (brood parasite) lays an egg in the nest of another female.

**brood reduction** The death of some siblings as a result of reduced parental care to enhance the fitness of surviving siblings.

**byproduct mutualism** When an individual's behavior enhances both its own fitness and the fitness of others.

**bystander** A third-party individual that detects a signal transmitted between a signaler and a receiver. Also called an **eavesdropper**.

**cache** Food stored in a hidden location for later retrieval.

**castes** Morphologically and behaviorally distinct individuals within a social group.

**challenge hypothesis** The hypothesis that male-male interactions increase plasma testosterone and thus sustain subsequent aggressive behavior.

**chemoreception** The process by which an animal detects chemical stimuli.

**classical conditioning** A type of learning in which a novel stimulus is paired with an existing stimulus and elicits a particular innate response. Eventually the novel stimulus alone elicits the same response as the existing stimulus. Also called **Pavlovian conditioning**.

**cleaner fish** Fish that feed on ectoparasites and the dead skin of other fish.

**coevolutionary arms race** The back-and-forth process of adaptation in one species favoring counteradaptation in another.

**cognition** The ability to generate and store mental representations of the physical and social environment to motivate behavior or solve problems.

**communication** The process in which a specialized signal produced by one individual affects the behavior of another.

**communication network** A communication system involving a signaler, a receiver, and at least one bystander.

**comparative method** An approach that examines differences and similarities between species to understand the



**comparative method** An approach that examines differences and similarities between species to understand the evolution of behavioral traits.

**compass** An instrument or capability that provides information about direction.

**competition** An interaction that results in a reduction in fitness for one or both individuals.

**conditional strategy** A strategy that an individual chooses based on its condition.

**cones** A type of photoreceptor for color vision.

**conspecific attraction** A phenomenon in which individuals are attracted to others, particularly during habitat selection.

**conspecific cueing** A hypothesized mechanism to explain conspecific attraction. A settler uses the presence of another individual as a cue to habitat quality.

**control group** In an experiment, the group that does not experience a manipulation. It provides a comparison to experimentally manipulated groups.

**cooperation** A behavior that benefits a recipient.

**cooperative behavior** A mutually beneficial interaction between individuals.

**cooperative breeding** In social groups, adults physiologically capable of reproducing forego breeding and instead help others raise offspring.

**correlation** Two variables that vary together predictably.

**cost-benefit approach** A method used to study behavioral adaptations in which the fitness benefits and costs of different traits are examined to determine which has the highest net benefit (calculated as benefit minus cost).

**cryptic coloration** Morphological coloration that matches the color of the environment to reduce detection by predators.

**cryptic female choice** A situation that occurs when a female influences the fertilization success of sperm from one male over that from others.

**dear enemy hypothesis** The hypothesis that territory owners will show reduced aggressive interactions toward territorial neighbors, compared to strangers, as a territory owner becomes more familiar with its neighbor.

**dendritic spines** Small protuberances on a dendrite that typically receive synaptic inputs.

**derived trait** A trait found in an organism that was not present in the last common ancestor of a group of two or more species. Also known as an **apomorphic trait**.

**descriptive statistics** Statistics used to summarize and describe measurements.

**dilution effect** A reduction in the probability of death as a result of associating with others.

**diminishing returns** A decline in instantaneous harvest rate as a food patch is depleted.

**direct familiarization** The ability of individuals to discriminate kin from non-kin through previous associations.

**direct fitness** Genes contributed to the next generation by an individual due to its own reproduction.

**direct material benefits** Material resources obtained by a female from mating with a particular male.

**direct material benefits** Material resources obtained by a female from mating with a particular male.

**direct reciprocity** A costly behavior from which an actor can benefit if the recipient of an altruistic act reciprocates in the future. Also known as **reciprocal altruism**.

**directional selection** A situation in which individuals with one extreme (highest or lowest) trait value in a population possess the highest fitness.

**dispersal** A relatively short-distance, one-way movement away from a site.

**disruptive selection** A situation in which individuals with either of two extreme (highest and lowest) trait values in a population possess the highest fitness.

**dominance effects (D)** The interaction between alleles at one locus, in which one allele can mask the expression (phenotype) of the other.

**dominance hierarchy** An organized social system with dominant and subordinate members.

**eavesdropper** A third-party individual that detects a signal transmitted between a signaler and a receiver. Also called a **bystander**.

**electroreception** The ability to detect weak electric fields.

**energetic costs of foraging** The energy used to exploit a patch and the metabolic costs incurred while feeding.

**epistasis (I)** Interactions between genes at different loci. Also called epistatic effects (I).

**epistatic effects (I)** Interactions between genes at different loci. Also called epistasis.

**ethogram** A formal description of an animal's behaviors.

**eusocial** The social structure of a species that lives in social groups, contains overlapping generations, has cooperative offspring care by nonparents, and has a reproductive division of labor.

**evolution** Changes in allele frequency or trait values in a population over time.

**evolutionary stable strategy (ESS)** A strategy that, if adopted by a population, cannot be invaded by another strategy because it yields the highest fitness.

**experimental method** An approach in which scientists manipulate or change a variable to examine how it affects the behavior of an animal.

**extended phenotype signal** A signal expressed beyond the body of an individual that often includes modification of the environment.

**extra-pair copulations (EPCs)** The copulations of a pair-bonded individual with a third individual outside the pair bond.

**extra-pair young** Offspring of a pair-bonded female produced outside the pair bond by a third-party male.

**female defense polygyny** A mating system in which a single male monopolizes and mates with two or more females.

**fitness** The relative survivorship and reproductive success (ability to produce viable offspring) of an individual.

**fixed action pattern** A behavior that is invariant, unlearned, and, once initiated, always completed.

**focal animal sampling** A data collection technique whereby a single focal individual is randomly selected and observed for a specified time period and all pertinent behaviors performed by the individual are recorded.

**frequency-dependent selection** An evolutionary process in which the fitness of a trait is related to its frequency in a population.

**game theory** A cost-benefit modeling approach in which an individual's fitness is affected by the behavior of others.

**gene expression** The process in which gene products are produced.

**generalist** A forager that consumes a wide variety of items in its diet.

**genetic mating system** A description of the mating system based on the actual number of sexual partners in a social mating system that contribute to a set of offspring.

**genetic quality hypothesis** The hypothesis that females that engage in multi-male matings can improve the fitness of their offspring via genetic mechanisms.

**genome** The complete DNA of an organism.

**genomics** Study of the structure, function, and evolution of genomes by examining gene expression.

**genotype (G)** The genetic makeup of an individual.

**geomagnetic compass** The ability to orient using the earth's magnetic field.

**giving-up density (GUD)** The density of food items in a food patch after being exploited by a forager.

**glucocorticoids** Hormones secreted by the adrenal gland in vertebrates in response to stressful situations.

**good genes** The alleles of a high-quality individual.

**group selection** A form of selection that favors particular groups of individuals over other such groups.

**group size effect** A commonly observed pattern in which the vigilance behavior of an individual declines as group size increases.

**gustation** The detection of dissolved chemicals, often within the mouth.

**habituation** The reduction and then lack of response to a stimulus over time.

**Hamilton's rule** An inequality predicting when altruism should evolve based on the fitness benefits and costs of the altruistic behavior and the degree of relatedness among individuals.

**Hamilton-Zuk hypothesis** The hypothesis that parasites and pathogens play an important role in sexual selection when secondary sexual traits are costly and condition dependent.

**handicap principle** The hypothesis that well-developed secondary sexual characteristics are costly because they handicap survival.

**handling time** The amount of time required to manipulate a food item so that it is ready to eat.

**haplodiploid genetic system** A genetic system with haploid males and diploid females.

**hatching asynchrony** A situation in which chicks in a clutch hatch on different days.

**hawk-dove model** A game theory model that examines the behavior of two individuals engaged in a contest over a resource.

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**hawk-dove model** A game theory model that examines the behavior of two individuals engaged in a contest over a resource.

**heritability ( $H^2$ )** The proportion of phenotypic variation in a population that is due to genetic variation.

**heritable** The characteristic of a trait that can be passed from parents to their offspring because it is genetically based.

**home range** An area of repeated use by an individual that is not defended from others.

**hotshot hypothesis** The hypothesis that males can increase their encounter rate with females by aggregating near an attractive male.

**hotspot hypothesis** The hypothesis that all males can benefit by aggregating in a location where they are likely to encounter many females.

**hypothesis** An explanation based on assumptions that makes a testable prediction.

**ideal free distribution (IFD) model** A model that explains how animals distribute themselves among habitats or food patches.

**image score** An assessment of an individual's propensity for helping others based on its observed prior behavior.

**imprinting** Rapid learning in young animals through observation of parents or other objects. Individuals are typically attracted to objects they imprint on.

**inbreeding avoidance hypothesis** The hypothesis that natal dispersal behavior minimizes the likelihood of inbreeding.

**inbreeding depression** A reduction in fitness as a result of mating with close relatives.

**inclusive fitness** The sum of an individual's direct and indirect fitness.

**indirect familiarization** The discrimination of kin from non-kin via phenotype matching.

**indirect fitness** The genes contributed to the next generation by an individual as a result of helping non-offspring kin produce additional offspring.

**indirect genetic benefits** Genetic benefits females can obtain for their offspring by mating with males that have high genetic quality.

**indirect reciprocity** A relationship in which helping individuals are more likely to receive help in the future because they have helped others.

**individual selection** Natural selection acting on individuals.

**inferential statistics** Statistics used in hypothesis testing to determine if there is a statistical difference between two or more sets of data.

**insight learning** Spontaneous problem solving without the benefit of trial-and-error learning.

**instantaneous sampling** A method of collecting behavioral data at regular time intervals. Also known as **scan sampling**.

**intergenerational migration** Migration that occurs over more than one generation.

**intersexual selection** Selection by one sex for members of the other sex for reproduction. Also known as **mate**

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**intersexual selection** Selection by one sex for members of the other sex for reproduction. Also known as **mate choice**.

**interspecific brood parasitism** A behavior in which a female (brood parasite) lays an egg in the nest of another species.

**intrasexual selection** A form of selection in which members of the same sex compete for access to the other sex for reproduction. Also known as **mate competition**.

**isodar** The line that results from plotting the number of individuals in one habitat against the number of individuals in another habitat at several points in time.

**isogamy** The production of gametes of the same size by all individuals.

**iteroparity** A life history strategy in which there are multiple reproductive events throughout the lifetime.

**juvenile hormones (JH)** In insects, a class of hormones produced by specialized endocrine glands. These hormones vary in a consistent manner with levels of parental care by females.

**kin selection** A form of natural selection in which individuals can increase their fitness by helping close relatives, who share the helper's genes.

**knockout technique** A procedure in which a single gene is rendered nonfunctional.

**lateral line system** In fish, a network of mechanoreceptors that provide hydrodynamic information.

**learning** A relatively permanent change in behavior due to experience.

**learning curve** A graphical representation of a change in learning over time.

**lek** A location where males aggregate and display to females.

**life history theory** Hypotheses that assume that natural selection will favor the evolution of behaviors and life history traits that maximize an individual's lifetime reproductive success.

**life history traits** Traits involved with growth, reproduction, and survivorship.

**linear dominance hierarchy** An organized social system in which an individual is dominant to each individual below and subordinate to all above it in rank.

**line chart** A graph in which data points are ordered on one or both axes and connected by lines. Also called a line graph.

**local enhancement** A strategy in which an individual uses the presence of another as a cue for focusing on a particular part of the environment.

**magnetoreception** The ability to detect and orient using magnetic fields.

**male dominance polygyny** A mating system in which a few males on a lek mate with many females.

**marginal value theorem** An optimal foraging model that predicts how long an individual should exploit a food patch.

**mate choice** Selection by one sex for members of the other sex for reproduction. Also known as **intersexual selection**.

**mate choice copying** A situation in which one individual observes and copies the mating decisions of another individual.

**mate competition** A situation in which members of the same sex compete for access to the other sex for reproduction. Also called **intrasexual selection**.

**mate guarding** A behavior in which a male remains close to his mate to prevent her from mating with rivals.

**mate guarding hypothesis** The hypothesis that selection favors males that mate with and guard one female over one or more reproductive cycles by remaining in close association with her.

**mating system** A description of the social associations and number of sexual partners an individual has during one breeding season.

**mean** The average value of a data set, determined by the sum of all the data divided by the number of data points.

**measure of central tendency** A number that indicates the centrality of the data values. Types include the mean, median, and mode.

**measures of dispersion** Methods of describing the variation in a data set. Common types include the range, variance, standard deviation, and standard error.

**mechanoreceptors** Sensory receptors sensitive to changes in pressure.

**median** The middle value of a data set, determined by ordering the data and finding the middle.

**migration** Relatively long-distance, two-way movement.

**mimicry** The adaptive resemblance of one species to another.

**missed opportunity costs of foraging** The fitness costs of not engaging in other activities while feeding.

**mobbing behavior** The harassment of a predator by two or more individuals.

**mode** The most common value of a data set, determined by ordering the data and counting the number of times each item occurs.

**monogamy** A mating system in which one female mates with one male.

**multilevel selection** A form of natural selection that can act simultaneously on individuals and groups. In some circumstances, selection may be stronger on groups than individuals.

**mutual-assessment game theory models** Game theory models that examine the behavior of two individuals engaged in a contest over a resource. Individuals are assumed to assess the relative fighting ability of their opponent and themselves in deciding how long to fight.

**natal dispersal** A one-time movement away from an individual's place of birth.

**natural selection** The process of differential reproduction and survivorship among individuals within a population.

**navigation** The process of determining a particular location and moving toward it.

**negative results** An outcome in which the null hypothesis is not rejected, and thus the alternate hypothesis is rejected.

**null hypothesis ( $H_0$ )** The statistical hypothesis that an observation results from chance. Also called the hypothesis



of no effect.

**numerical competency** The ability to recognize numerical quantities.

**nuptial gift** A physical resource such as a food item that an individual provides to a potential mate to enhance mating success.

**observational method** An approach in which scientists observe and record the behavior of an organism without manipulating the environment or the animal.

**odorant** A gaseous compound that is perceived as odorous.

**olfaction** The detection of airborne chemical stimuli.

**operant chamber** An enclosure used to study behavioral conditioning. Also known as a **Skinner box**.

**operant conditioning** A process in which an animal learns to associate a behavior with a particular consequence.

**operational sex ratio** The ratio of the number of sexually receptive males to sexually receptive females in a population.

**optimal behavior** The behavior that maximizes fitness in an optimal foraging theory model.

**optimal foraging theory** An approach to studying feeding behavior that assumes that natural selection has favored feeding behaviors that maximize fitness.

**optimal trait value** The trait value that confers the highest fitness in a population in a particular environment.

**orientation** The process of determining and maintaining a proper direction.

**ornaments** Exaggerated morphological traits used to attract mates.

**parental care** Behaviors by a parent to enhance the fitness of offspring, including incubation, feeding, and defense.

**parental investment** Any investment by a parent in an offspring that enhances the offspring's fitness at the cost of the parent's ability to invest in other offspring.

**parental investment theory** The hypothesis that the sex that pays the higher cost of parental investment should be choosier when it comes to mates.

**parent-offspring conflict theory** The hypothesis that parents and their dependent offspring are under different selection pressures: parents should maximize their lifetime reproductive fitness, while offspring should maximize the energy and protection they currently receive from their parents in order to survive to reproductive age.

**parent-offspring regression** A statistical technique used to examine the similarity between parents and their offspring in terms of the traits they possess.

**Pavlovian conditioning** A type of learning in which a novel stimulus is paired with an existing stimulus and elicits a particular response. Eventually the novel stimulus alone elicits the same response as the existing stimulus. Also called **classical conditioning**.

**peer review** A process in which editors of scientific journals ask experts to review a submitted paper to determine whether to accept or reject it for publication.

**personality** Consistent relative differences in behavior among individuals over time or across different environmental contexts.

environmental contexts.

**phenotype (P)** The observable traits of an individual.

**pheromones** Volatile, organic, species-specific compounds that affect the behavior of conspecifics.

**photoreceptor** Specialized neurons that are sensitive to light and function as visual receptors.

**phylogeny** A branching diagram showing hypothesized evolutionary relationships among species. Sometimes called a phylogenetic tree.

**pie chart** A graph that summarizes data in a circle with different sectors representing different data categories.

**pleiotropy** A situation in which a single gene affects more than one phenotypic trait.

**plesiomorphic trait** A trait found in the common ancestor of two or more species. Also called an **ancestral trait**.

**plural breeding** A mating system of social species in which multiple males and multiple females associate and mate with one another and produce young in one breeding attempt. Also known as **polygyny**.

**polyandry** A mating system in which a single female associates and mates with multiple males.

**polygyny** A mating system of social species in which multiple males and multiple females associate and mate with one another and produce young in one breeding attempt. Also known as **plural breeding**.

**polygyny** A mating system in which a single male associates and mates with multiple females.

**polygyny threshold model** A model that predicts the occurrence of polygyny based on the amount of resources available to females in male territories.

**predation risk cost** The fitness cost associated with the likelihood of being killed by a predator. Often equated with the probability of being killed by a predator.

**predator harassment** Interactions with a predator to deter attack. Such behavior can involve rapid movements, loud vocalizations, and throwing or kicking objects at the predator.

**primary literature** The original source of scientific information, typically peer-reviewed scientific journals.

**primary sexual characteristics** The genitalia and organs of reproduction.

**process of science** Observing events, organizing knowledge, and providing explanations through the formulation and testing of hypotheses.

**producer** An individual in a group that searches for food.

**profitability** For a food item, the energy it contains divided by the handling time.

**prolactin** A hormone that influences parental care in vertebrates.

**promiscuity** A mating system in which both males and females mate with multiple partners in the absence of pair bonds.

**proximate explanation** An explanation that focuses on understanding the underlying mechanisms of a behavior.

**public information** Information obtained from the activity or performance of others about the quality of an environmental parameter or resource.

**pursuit-deterrence hypothesis** The hypothesis that advertisement behavior informs a predator that it has been detected and so pursuit is not likely to be successful.

**QTL mapping** A statistical technique that combines genetic information with trait information to determine which regions of the genome contain the genes that influence the trait QTLs.

**quantitative trait loci (QTL)** Stretches of DNA that either contain or are linked to genes influencing a trait such as behavior.

**quitting harvest rate** The forager's instantaneous harvest rate when it leaves a food patch.

**range** The difference between the highest and lowest measurements of a data set.

**reciprocal altruism** A costly behavior from which an actor can benefit if the recipient of an altruistic act reciprocates in the future. Also known as **direct reciprocity**.

**reduction** An ethical guideline that promotes limiting the number of animals subject to disturbance in research or teaching.

**refinement** An ethical guideline that involves improving procedures and techniques to minimize pain and stress for animals.

**replacement** An ethical guideline that encourages the use of computer modeling, recordings, or other approaches in place of actual animals.

**reproductive skew** Variation in reproductive success among members of a group.

**research question** A formal statement of an unknown that begins the scientific method.

**resource defense polygyny** A mating system in which a male mates with multiple females that are attracted to resources he defends.

**resource holding potential (RHP)** The ability to win an aggressive encounter.

**rods** A type of photoreceptor that is sensitive to low light levels.

**rover** One type of genetic and behavioral variant in fruit flies. Larval rovers have longer foraging trails than sitters in the presence of food and are more likely to leave a food patch.

**runaway process** An evolutionary process in which a male trait coevolves with a female preference for it and becomes increasingly exaggerated.

**sample** A subset of a population or group that is chosen to be representative of the entire population being studied.

**sample mean** The average of the data within a sample.

**scan sampling** A method of collecting data in which data are collected from all individuals at regular time intervals. Also known as **instantaneous sampling**.

**scatter plot** A graph that displays the relationship between two measured variables. Each data point represents the value of both the x and y variables.

**scientific misconduct** The violation of ethical behavior standards in science. It includes the falsification or fabrication of data, purposefully inappropriate analysis of data, and plagiarism.

**scientific theories** Hypotheses that have been tested many times, by different scientists, and have not been

rejected. Scientific theories provide a conceptual framework that explains many phenomena and are well supported by observations and experimental tests.

**scramble competition** The indirect competition of individuals to find and secure copulations with multiple mates.

**scrounger** Individuals in a group that exploit the food discoveries of others.

**search image** The distinctive visual features of a single prey type, which, once learned, can enhance prey detection.

**secondary literature** A report, which often appears in newspapers, magazines, and books, that summarizes and interprets the primary literature.

**secondary sexual characteristics** Morphological differences between the sexes that are not directly involved in reproduction.

**selection experiment** An experiment in which different groups of individuals are subjected to differential selection on a trait.

**self-assessment game theory models** Game theory models that examine the behavior of two individuals engaged in a contest over a resource. Each individual is assumed to assess its resource holding power in deciding how long to fight.

**selfish herd hypothesis** The hypothesis that a predator is more likely to kill a member on the outside of a group because it will encounter outside individuals first.

**semelparity** A life history strategy in which reproduction occurs once in the lifetime.

**sensory bias hypothesis** The hypothesis that female mating preferences are a byproduct of preexisting biases in a female's sensory system.

**sex role-reversed species** A species in which females compete for males that invest heavily in parental care.

**sexual conflict** The differential selection on males and females to maximize their fitness.

**sexual deception hypothesis** The hypothesis that males will produce deceptive signals to females in order to enhance their own reproduction.

**sexual dimorphism** Morphological differences between the sexes.

**sexual selection** A form of natural selection that acts on heritable traits that affect reproduction.

**signal** An evolved trait that is selected for its effect on the behavior of a receiver.

**sister species** Two species that are more closely related to one another than to any other species; species that share a recent common ancestor.

**site fidelity** Individuals that remain at or return to a previous location to breed.

**sitter** One type of genetic and behavioral variant in fruit flies. Larval sitters have shorter foraging trails than rovers in the presence of food and are less likely to leave a food patch.

**Skinner box** An enclosure used to study behavioral conditioning. Also known as an **operant chamber**.

**social group** A set of individuals that live near and associate with one another.

**social mating system** The social associations and presumed mating behavior of individuals based on those associations.

**social queuing** A process in which subordinates eventually move up the social ladder as they age.

**sociality** The tendency to live and associate with others.

**specialist** A forager that has a narrow diet.

**sperm competition** A situation that occurs when the sperm of different males compete to fertilize eggs.

**stabilizing selection** A mode of selection in which individuals with intermediate trait values in a population have the highest fitness in a particular environment.

**standard deviation (S)** The square root of the variance.

**standard error (SE)** The standard deviation of the data divided by the square root of the sample size.

**star compass** The use of stars or constellations for orientation.

**statistics** The branch of applied mathematics that uses probability theory to analyze and interpret numerical data.

**sun compass** The use of the sun for orientation.

**teaching** The active participation of an experienced individual in facilitating learning by a naïve conspecific.

**territorial cooperation hypothesis** The hypothesis that two individuals (one of each sex) can better defend a critical resource, such as a safe refuge, than can a single individual, and thus selection may favor pair formation and shared defense.

**territory** An area defended to obtain the exclusive use of the resources it contains.

**testosterone** A steroid hormone produced in the gonads and regulated by the hypothalamus and pituitary gland.

**time budget** A summary of the total time and relative frequency of different behaviors of an individual.

**trial-and-error learning** Learning to solve a problem through repetition.

**ultimate explanation** An explanation of behavior that requires evolutionary reasoning and analysis.

**variance ( $S^2$ )** A non-negative number that provides information on spread in the data. The larger the variance, the more dispersion there is.

**vigilance behavior** A behavior in which an individual scans the environment for predators.

**volatile** A substance that has the capability of evaporating, or becoming gaseous.

**waggle dance** Behavior performed by a honeybee scout that recruits workers to exploit a food source.

**weapons** Exaggerated morphological traits used in competition with individuals of the same sex.

**wild type** The typical form of an organism or gene in nature.

**winner effect** A phenomenon in which winning an aggressive interaction enhances the likelihood of winning a subsequent interaction.

**winner-challenge effect** A situation in which winning an aggressive interaction increases plasma testosterone.

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# CHAPTER 16

## Cooperative Behavior

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### Concepts

- 16.1 [Inclusive fitness theory explains the evolution of cooperation among related individuals](#)
- 16.2 [Individuals can discriminate kin from non-kin](#)
- 16.3 [Cooperative behavior among unrelated individuals involves byproduct mutualisms or reciprocity](#)
- 16.4 [Kinship and ecological constraints favor cooperative reproduction](#)

### Features

- |                        |   |
|------------------------|---|
| Scientific Process     | 16.1 <a href="#">Reputation formation in great apes</a> |
| Applying the Concepts  | 16.1 <a href="#">Human altruism and reputations</a>     |
| Quantitative Reasoning | 16.1 <a href="#">Food sharing in killer whales</a>      |

We live in a semirural area with a wooded backyard that attracts a diverse array of wildlife, including deer, coyotes, foxes, woodpeckers, and turtles. One of the more interesting sights occurs in spring, when flocks of 20 to 30 turkeys wander through, searching for acorns, seeds, and berries. Because turkeys are sexually dimorphic, we can see that almost all the individuals are females, but there are always one or two males. While the females spend most of the time foraging, the males often engage in courtship display—known as strutting—in which they spread and hold their tail feathers vertically, drop their wings to the ground, puff up their back and breast feathers, and bring their heads and necks into an S formation (Figure. 16.1). When two males are present, they often stand near one another and both display. Are they competing for the attention of females or cooperating with one another?



FIGURE 16.1. Male turkey display. Two males strutting.

In this chapter, we'll learn the answer as we discuss cooperation, a common behavior in many social species. We'll examine types of cooperative behavior, in which individuals cooperate with one another, and how cooperation can evolve.

### Video: Male turkey coalitions

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## 16.1 Inclusive fitness theory explains the evolution of cooperation among related individuals

### Learning Objectives

After reading this section, you should be able to

- distinguish direct and indirect aspects of inclusive fitness; and
- predict when cooperation should occur, using Hamilton's rule.

**Cooperation** occurs when an individual's behavior benefits the fitness of another individual and evolves in part because of this benefit. Many cooperative behaviors are costly, or **altruistic**; that is, they reduce the fitness of the individual performing the behavior. Because it is not obvious how such behaviors can evolve under natural selection, their evolution can be difficult to explain. Recall from [Chapter 3](#) that theoretical explanations of the evolution of cooperation involve inclusive fitness, an idea formalized by William Hamilton ([Hamilton 1964](#)). The inclusive fitness of a focal individual is the sum of its direct and indirect fitness. Direct fitness is determined by the focal individual's own reproductive success, while indirect fitness is determined by how the focal individual's behavior enhances the reproduction of related individuals. Hamilton argued that natural selection will favor individuals that maximize their inclusive fitness, and so cooperative behaviors that increase the reproductive success of relatives can increase in a population: cooperative behaviors, then, can evolve. When an individual helps a relative produce more offspring, the actor and recipient share genetic relatives. By helping a relative, the cooperating individual is helping pass identical copies of its own alleles on to the next generation indirectly through the additional reproduction of a relative. The cooperating individual has increased its inclusive fitness because of its cooperative behavior.

### Hamilton's rule

Hamilton proposed that for altruism to evolve, the additional fitness benefits ( $B$ ) obtained by the recipient must be greater than the fitness cost ( $C$ ) to the actor, adjusted for the degree of relatedness ( $r$ ) between the two individuals ([Table 16.1](#)). The degree (or coefficient) of relatedness is the probability that two individuals have inherited the same allele at a particular locus from a common ancestor. Hamilton formalized this relationship in an inequality ([Hamilton 1964](#)) that is known as **Hamilton's rule**:

$$\text{Altruism can evolve when } B \times r > C$$

This inequality makes a prediction about when altruism can evolve, but parameters  $B$  and  $C$  can be difficult to estimate. Many tests of Hamilton's rule therefore examine a more general prediction: helping behavior should be most common between close relatives (when  $r$  is relatively high), less common between distant relatives (when  $r$

is low), and rare between unrelated individuals (when  $r$  is 0). Because degree of relatedness between individuals is central to Hamilton's rule, it is often referred to as kin selection.

**TABLE 16.1 Degree of relatedness.** Coefficient of relatedness ( $r$ ) for different relationship types among pairs of individuals.

Relationship	Coefficient of Relatedness ( $r$ )
Parent–offspring	0.50
Sibling–sibling	0.50
Grandparent–grandchild	0.25
Aunt/uncle–nephew/niece	0.25
First cousins	0.125
Unrelated individuals	0

### FEATURED RESEARCH Belding's ground squirrel alarm calls

In a classic test of kin selection, Paul Sherman studied alarm-calling behavior in Belding's ground squirrels (*Spermophilus beldingi*) ([Sherman 1977](#)). These rodents live in high-density populations and interact frequently in subalpine meadows in western North America ([Figure 16.2](#)). Adult females and males live in very different social environments. Females tend to be surrounded by female relatives, because juvenile females disperse very short distances from their natal burrow. In contrast, males tend to be surrounded by unrelated squirrels because juvenile males disperse more than 250 m from their natal burrow, and adult males move an additional 150 m away from their mate's burrow when the offspring are born.







**FIGURE 16.2. Belding's ground squirrels.** A social mammal that lives in large colonies.

Ground squirrels are attacked by a variety of animals and produce specific vocalizations, or alarm calls, in response to predators such as long-tailed weasels (*Mustela frenata*) and badgers (*Taxidea taxus*). Upon hearing an alarm call, individuals will typically run to the nearest burrow or scan the environment, behaviors that reduce their risk of predation. But alarm calls also entail a risk: producing a vocalization can attract a predator to the caller.

#### Video: Belding's ground squirrel alarm calling

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Video: Belding's ground squirrel alarm calling

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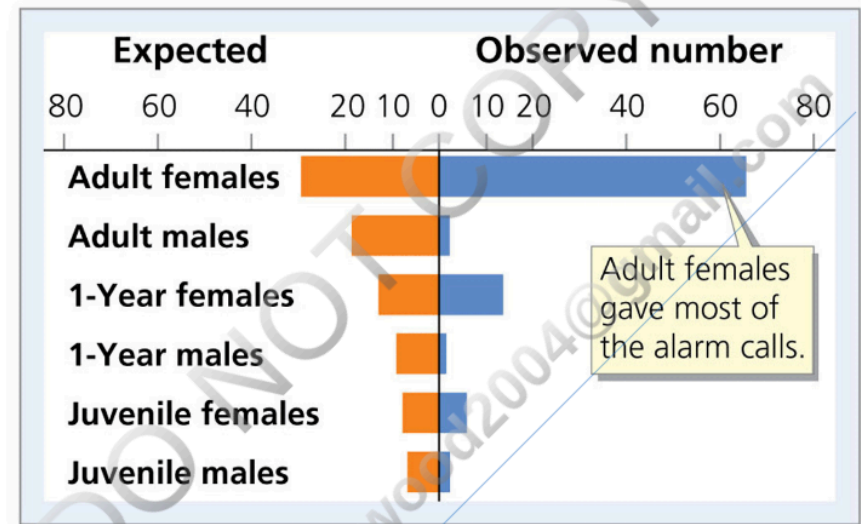
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To determine if kin selection can explain the evolution of alarm calling behavior, Sherman studied one ground squirrel population over three years, individually marking hundreds of individuals. He recorded 102 occasions

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when a predator was present while squirrels were active; 22 marked squirrels were subsequently stalked or chased. He also noted the first squirrel to produce an alarm call.

He found that adult females were significantly more likely to give the first alarm call than were adult males or juveniles (Figure 16.3). In fact, adult males rarely gave the first alarm call when a predator was present. Sherman also noted that individuals paid a fitness cost of calling: significantly more calling squirrels were hunted by predators than were noncallers, and more callers were killed. Three that were killed gave an alarm call just before being attacked.



**FIGURE 16.3. Ground squirrel alarm calls.** Observed (blue) and expected (orange) number of first alarm calls given based on the numbers of different individuals in each age class in the population. Adult females gave significantly more calls than expected, whereas adult males gave significantly fewer. (Source: Sherman 1977)

Sherman concluded that kin selection can explain the observed variation in alarm-calling behavior because adult females, and not males, are surrounded by close relatives. If alarm calls help increase the survival of close relatives, this behavior could provide genetic benefits to the female callers. Alarm calls are costly to produce because individuals who give them suffer higher predation risk than noncallers, and so adult males, who are not surrounded by close relatives, rarely produce these calls.

These results demonstrate that kin selection can explain variation in cooperative behavior when animals face predation risk. Next, we examine cooperation in the context of reproduction.

#### FEATURED RESEARCH Altruism in turkeys

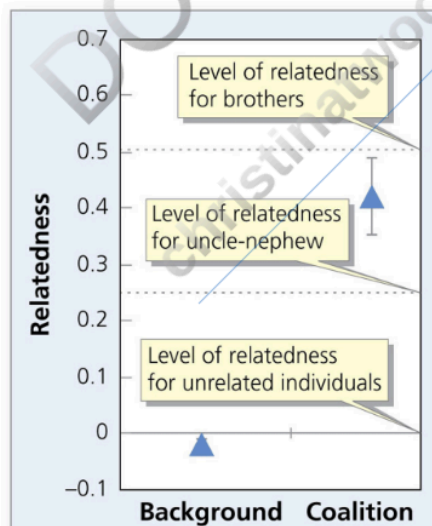
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Although measuring all the parameters of Hamilton's rule to test its prediction more precisely seems a daunting task, Alan Krakauer attempted just that in turkeys (*Meleagris gallopavo*). These large birds (over 1 m in length) live in open fields and woodlands throughout much of North America. As we noted at the beginning of this chapter, turkeys often form male display partnerships in which a pair, called a coalition, display together to court and defend females against other males. However, only the dominant coalition member mates. Why does the subordinate bird display with another male when doing so has no direct reproductive fitness benefit? One possibility is that the males are closely related and the subordinate individual obtains indirect fitness benefits via kin selection (Watts & Stokes 1971).

Krakauer tested this idea by studying a population at Hastings Natural History Reservation near Carmel, California (Krakauer 2005). He captured and uniquely marked 126 turkeys with colored wing tags and collected blood samples to conduct DNA analysis. DNA was genotyped to determine both relatedness among individuals and paternity of offspring, with the latter allowing him to quantify the males' reproductive success. To facilitate rapid location of birds and their nests, dozens of subjects were fitted with radio transmitters.

Turkeys were located regularly to observe courtship behavior and associations among males. Coalitions were defined as pairs of males within 2 m of each other that displayed at least twice to a female. The dominant male was identified as the turkey that strutted the most. Solitary males, on the other hand, were those adults that did not meet these criteria and were observed displaying alone to a female at least twice.

The combination of behavioral observations and genetic data allowed Krakauer to calculate all three parameters in Hamilton's rule. The mean degree of relatedness between individuals was 0.42, slightly below the value for full brothers (0.50) but significantly higher than the value for any two random males in the population (Figure 16.4). Thus, he concluded that coalitions were composed of very close relatives.



**FIGURE 16.4. Relatedness in turkey coalitions.** Males in coalitions are closely related ( $r = 0.42$ ), while random (background) pairs of males in the population are unrelated. Data are mean  $\pm$  SE. (Source: Krakauer 2005)

Krakauer found that the subordinate males in these coalitions fathered no offspring, but that dominant males fathered an average of 7.0. In contrast, solo males sired, on average, only 0.9 offspring. We can now plug these values into Hamilton's rule. First, the additional fitness benefit ( $B$ ) that the dominant obtained from the cooperation it received from a subordinate was  $(7.0 - 0.9)$ , or 6.1 offspring per male. The fitness cost of helping ( $C$ ) was 0.9, the number of offspring that the subordinate could achieve as a solo male. Finally, the average relatedness ( $r$ ) between coalition members was 0.42. In sum,

$$B \times r = 6.1 \times 0.42 = 2.56 > 0.9 = C$$

Hamilton's rule is satisfied for subordinate males:  $B \times r$  is greater than  $C$ , and the fitness of altruistic subordinates is higher (thanks to kin selection) than the fitness of nonaltruistic solo males. In this case, subordinate males indeed obtain higher fitness by forming a coalition with, and helping, a close relative reproduce than they would if they attempted to reproduce on their own.

As these examples illustrate, kin selection is an important concept for understanding the evolution of cooperative behavior among close relatives in a variety of species. For it to explain cooperation, however, actors must bias their cooperative behavior toward their kin.

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As these examples illustrate, kin selection is an important concept for understanding the evolution of cooperative behavior among close relatives in a variety of species. For it to explain cooperation, however, actors must bias their cooperative behavior toward their kin.

## 16.2 Individuals can discriminate kin from non-kin

### Learning Objectives

After reading this section, you should be able to

- describe the role of kin discrimination in Hamilton's rule and
- distinguish kin discrimination via direct versus indirect familiarization.

Hamilton's rule tacitly assumes that individuals can discriminate kin from non-kin so that altruistic behaviors can benefit relatives. Numerous studies show that individuals, when given a choice, prefer to associate with kin over non-kin in a nonmating context but display the opposite preference when seeking mates (e.g., [Ward & Hart 2003](#); [Widdig 2007](#); [Gherardi, Aquiloni, & Tricarico 2012](#)). These studies demonstrate that animals have the ability to discriminate kin from non-kin. But how?

### Kin discrimination

Two mechanisms are thought to provide explanations for kin discrimination ability. First, an individual can learn to discriminate kin from non-kin through previous associations, a process called **direct familiarization** ([Tang-Martinez 2001](#)). In many species, siblings are raised together or remain close to their parents for an extended period and so have the opportunity to learn the phenotypes of these close relatives. Second, individuals could discriminate kin from non-kin via phenotype matching, or **indirect familiarization**. In this process, individuals are assumed to use a reference phenotypic cue from themselves or a known close relative (like a parent). One such cue might be a chemical odor profile. An individual then assesses the degree of similarity between the reference and the cue in others: more closely related individuals should have a higher degree of similarity in the cue.

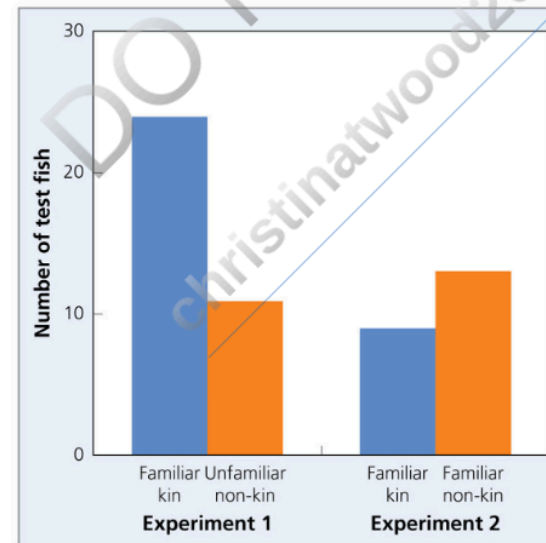
How can we distinguish these possibilities? One clear distinction between these mechanisms is that direct familiarization requires prior association, while indirect familiarization does not. Let's examine two studies that have tested how individuals discriminate between kin and non-kin.

## FEATURED RESEARCH Direct familiarization and kin discrimination in sticklebacks

Schooling with kin often leads to lower levels of aggression than schooling with non-kin ([Brown & Brown 1993](#)). Not surprisingly, several studies have shown that fish, such as three-spined sticklebacks (*Gasterosteus aculeatus*), prefer to school with kin ([Frommen & Bakker 2004](#); [Ward & Hart 2003](#)). Joachim Frommen, Corinna Luz, and Theo Bakker conducted a simple experiment to examine how sticklebacks might recognize kin ([Frommen, Luz, & Bakker 2007](#)).

They reared two sets of juveniles in different conditions over five weeks: one was raised with kin (full siblings) only, while the other was raised with both kin (full siblings) and non-kin. In the first test, the researchers placed a single kin-reared focal fish in the central compartment of an aquarium. Two stimulus schools were present on either side of the tank, which allowed both visual and olfactory information to be shared between all compartments: one school contained seven kin, while the other contained seven unrelated individuals. The research team recorded how much time the focal fish spent near each school. Their findings showed that individuals spent significantly more time on the side that contained familiar kin, a hallmark of kin discrimination.

Next, using the same setup, focal fish reared with both kin and non-kin were presented with one stimulus school of familiar kin and one of familiar non-kin. In this second test, focal fish showed no preference for schooling with kin ([Figure 16.5](#)), which suggests that sticklebacks use direct familiarization based on previous association when selecting shoalmates. In nature, sticklebacks spend several days in a nest after hatching, a time in which they may learn their siblings' phenotypes.





**FIGURE 16.5. Kin discrimination experiment in sticklebacks.** In Test 1, more focal fish preferred to associate with familiar kin over unfamiliar non-kin. In Test 2, focal fish showed no significant preference between familiar kin and familiar non-kin. (Source: [Frommen, Luz, & Bakker 2007](#))

This study indicates that sticklebacks become familiar with other individuals at an early age based on prior association with them, but it does not reveal how they identify those individuals. Because the test fish had access to both visual and chemical information from the stimulus shoals, either factor could potentially explain such recognition. The researchers postulate that sticklebacks use olfactory information to discriminate, given the sophistication of this sensory system in fish ([Chapter 5](#)), but this hypothesis awaits testing.

The next study focuses more directly on olfactory information as the basis for kin discrimination in an insect.

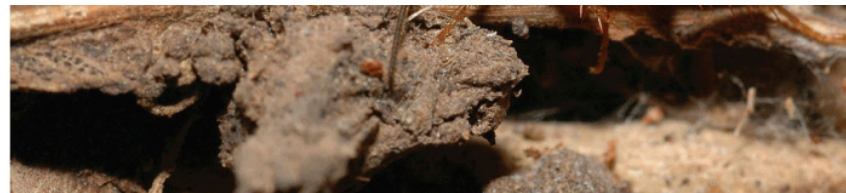
## FEATURED RESEARCH Indirect familiarization and kin discrimination in cockroaches

Many insects live in social groups with close relatives and can discriminate kin from non-kin ([Gherardi, Aquiloni, & Tricarico 2012](#)). Kin discrimination in insects is thought to involve an assessment of chemicals found on an individual's body surface, or cuticle. One diverse class of compounds that may play a role in individual discrimination is cuticular hydrocarbons (CHCs). These hydrocarbons range in chain length from one to several dozen carbon atoms, and the number and relative proportion of different CHCs present (known as a CHC profile) can vary greatly among individuals in a population ([Singer 1998](#)).

Mathieu Lihoreau and Colette Rivault investigated kin discrimination ability in nymphs of the urban cockroach (*Blattella germanica*) ([Figure 16.6](#)) ([Lihoreau & Rivault 2009](#)). In this nocturnal species, females mate once and produce repeated batches of full siblings that develop through six nymphal instars (distinct developmental stages between molting periods). Offspring often share a shelter to reduce physiological costs related to water loss and usually remain in their hatching area for up to several weeks while they mature. A total of 25 CHCs have been identified in this species, and CHC profiles of siblings are more similar to one another than they are to those of non-kin ([Lihoreau & Rivault 2009](#)), suggesting that they potentially play an important role in kin discrimination.



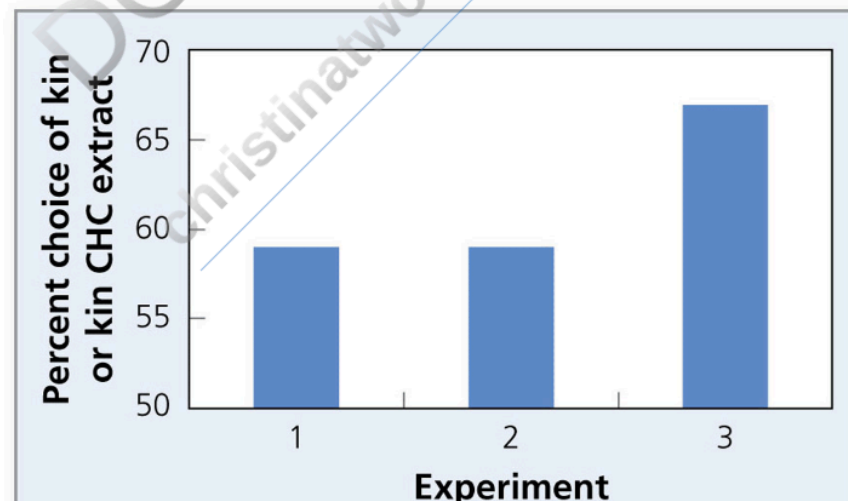
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**FIGURE 16.6. Urban cockroach.** An insect that lives in social groups with close relatives.

In three experiments, Lihoreau and Rivault investigated individuals' choice of social partners. In the first experiment, they reared nymphs in groups of siblings. To test nymph social preference, they placed individuals in the center of a petri dish that contained two potential resting sites (small cylinders). One resting site contained 15 sibling nymphs that had been reared with the test individual, and the other contained 15 nonsibling nymphs. The second experiment imposed the same conditions, but each test subject had been reared in isolation. In the third experiment, the resting-site nymphs were replaced with filter paper scented with CHC extracts of siblings and nonsiblings, respectively. In each experiment, a fine mesh covered the cylinder but allowed the test nymphs to have antennal contact with either the individuals or the filter paper in each site. The research team recorded the cylinder that each test nymph settled on (i.e., its choice of resting site).

In all the experiments, a significantly higher number of nymphs selected the site that contained either kin or kin's CHC extract ([Figure 16.7](#)). Because individuals without prior association with kin also showed this preference, and because nymphs preferred to associate with sibling CHC extract over non-kin CHC extract, these experiments demonstrate kin discrimination via indirect familiarization based on CHC profiles. Nymphs apparently use the CHC profiles of individuals to discriminate kin from non-kin and do so even with no prior association. How this is done, however, is still not clear.



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**FIGURE 16.7. Kin discrimination in cockroaches.** In all experiments, individuals preferred to associate with kin (Experiments 1 and 2) or with their kin's CHC extract (Experiment 3). (Source: [Lihoreau & Rivault 2009](#))

Many additional studies demonstrate that kin selection, facilitated by kin discrimination, helps explain cooperation among relatives ([Abbot et al. 2011](#)). But kin selection is only part of the explanation for the evolution of cooperative behavior, because it cannot explain cooperation that occurs among unrelated individuals.

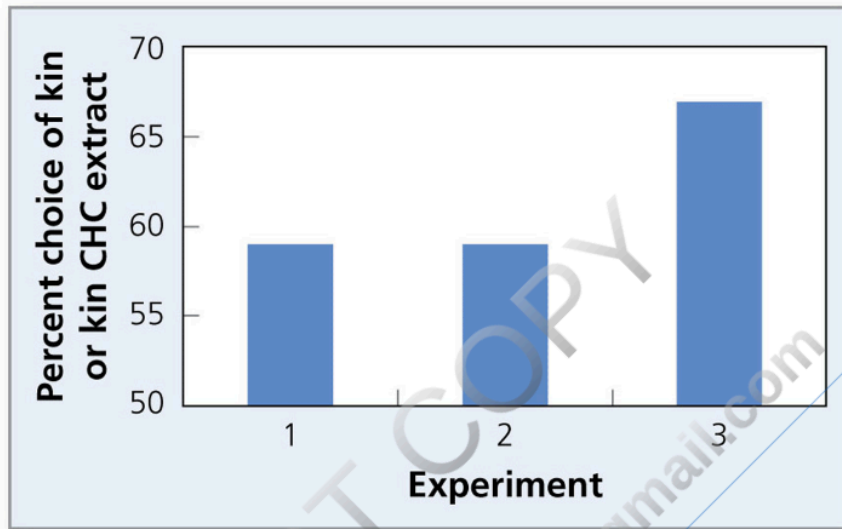
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Many additional studies demonstrate that kin selection, facilitated by kin discrimination, helps explain cooperation among relatives ([Abbot et al. 2011](#)). But kin selection is only part of the explanation for the evolution of cooperative behavior, because it cannot explain cooperation that occurs among unrelated individuals.

## 16.3 Cooperative behavior among unrelated individuals involves byproduct mutualisms or reciprocity

### Learning Objectives

After reading this section, you should be able to

- explain why it is difficult for cooperation to evolve in the prisoner's dilemma scenario,
- describe the tit-for-tat strategy,
- differentiate between the prisoner's dilemma and the snowdrift game,

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- distinguish direct from indirect reciprocity, and
- explain the role of reputations in the evolution of cooperation through indirect reciprocity.

For cooperation to evolve among unrelated individuals, we need to focus on the direct benefits of inclusive fitness. We must answer the following question: How can an individual enhance its direct fitness by cooperating with an unrelated individual? One possibility is that apparently cooperative behavior is actually selfish behavior. For instance, in vertebrates such as chimpanzees (*Pan troglodytes*), African wild dogs (*Lycaon pictus*), and Harris's hawks (*Parabuteo unicinctus*), nonrelatives often hunt together, and individuals obtain higher fitness (via increased feeding rates) when doing so ([Bednarek 1988](#); [Boesch 1994](#); [Creel & Creel 1995](#)). As a byproduct of engaging in cooperative hunting, all group members hunt more effectively or on a wider range of prey than they can when hunting alone. That is, the decision to hunt with others has a self-serving outcome. In these cases, an individual's behavior can enhance both its own and others' fitness, a phenomenon known as **byproduct mutualism**, and natural selection will favor such apparently cooperative behavior. Other examples of byproduct mutualisms include cooperative defense of a resource such as a territory ([Mosser & Packer 2009](#)) and antipredator benefits of associating with others such as mobbing behavior ([Chapter 9](#)).

### Direct reciprocity

However, many other forms of cooperation among unrelated individuals involve a fitness cost to the cooperative individual and so are unlikely to be a byproduct mutualism. For example, in many birds, ungulates, and primates, one individual will remove ectoparasites from another (often a nonrelative), a behavior known as **allogrooming**. This behavior is altruistic because it benefits the recipient while incurring a cost of time and effort for the groomer. How can such behavior evolve?

Robert Trivers offered one answer: **direct reciprocity (or reciprocal altruism)** ([Trivers 1971](#)), a costly behavior from which an actor can benefit if the recipient of an altruistic act reciprocates in the future. Trivers argued that helping behavior can evolve between unrelated individuals only when the benefit of helping exceeds the cost. For him, the evolution of cooperation requires that two individuals interact at least twice so that each helps and subsequently is helped. If the benefit received exceeds the cost, individuals that help will obtain higher fitness through the repeated interaction than will nonhelpers, and helping behavior can spread in a population.

Trivers recognized that reciprocal altruism is subject to cheating: an individual that receives help but then does not reciprocate will obtain a fitness benefit but pay no cost. This temptation to cheat can in fact prevent the evolution of helping, as we see next.

### The prisoner's dilemma

An illustration of the temptation to cheat is the prisoner's dilemma, a game theory scenario popularized in economics and political science that illustrates why the evolution of cooperation is difficult ([Trivers 1971](#)).

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Imagine that the police have arrested two criminals. There is evidence to convict them of a minor crime, but they are suspected of also committing a more major offense. The police need one of the criminals to provide information in order to charge and convict one suspect of the major crime. The criminals had previously agreed not to rat on each other if captured, but they are separated by the police and cannot communicate. Each is offered the same deal: if they testify (defect) against the other and the other remains silent (and thus cooperates with their partner),

## 16.4 Kinship and ecological constraints favor cooperative reproduction

### Learning Objectives

After reading this section, you should be able to

- describe the role of kinship and ecological constraints as factors that can favor the evolution of cooperative breeding,
- differentiate between habitat saturation and social queuing as types of ecological constraints that can favor cooperative breeding, and
- distinguish the haplodiploidy hypothesis from the kinship and ecological constraints hypothesis to explain the evolution of sterile castes.

In many species, individuals in groups cooperatively raise offspring. In such groups, there can be tremendous variation in the relative reproductive success of adults, measured as **reproductive skew**. In groups with low reproductive skew, all adults produce similar numbers of offspring. However, many groups exhibit high reproductive skew because breeding is restricted to a few adults, often just a single pair, and all the others defend group resources and care for the offspring.

How can we explain the evolution of cooperative behavior in groups with high reproductive skew? We address this question first in vertebrates and then in social insects.

### The evolution of cooperative breeding in vertebrates

In hundreds of species of birds, mammals, and fish, social groups often exhibit high reproductive skew because many adults do not reproduce but instead spend time and effort caring for the offspring of others, a phenomenon known as **cooperative breeding** (Clutton-Brock 2002). These “helpers” do not breed themselves but provide parental care to others’ offspring in the form of incubation, food provision, territorial defense, and antipredator behavior. Helpers are clearly exhibiting altruistic behavior: they pay the energy costs associated with parental care, sacrifice the chance to breed, and enhance the fitness of others.

Two important factors explain the evolution of nonreproductive helpers. First, in many species, helpers are closely related to the breeding pair; often, they are older offspring of that pair. As such, they are helping relatives and accrue indirect fitness benefits via kin selection. Second is the existence of ecological constraints. Attempting to breed can entail considerable risk based on environmental conditions. For instance, there may be a lack of available breeding sites or very high predation risk when searching for a suitable breeding site. If few breeding

sites are available in the environment, or if it is risky to leave a group to attempt to breed, it can be more beneficial for an individual to help a breeding pair raise related offspring (Emlen 1982). As we saw in Chapter 15, belonging to a group provides numerous fitness benefits to individuals. Opting to stay in a group to help raise others' offspring avoids the potential high cost of attempting to find and establish a new breeding territory and simultaneously provides benefits of social living. Essentially, individuals can obtain higher fitness by waiting for better conditions in the future, when new breeding sites or opportunities may become available.

Let's examine cooperative breeding examples in mammals, birds, and fish to see how the relative importance of kinship and ecological constraints vary across species.

## FEATURED RESEARCH Cooperative breeding in meerkats

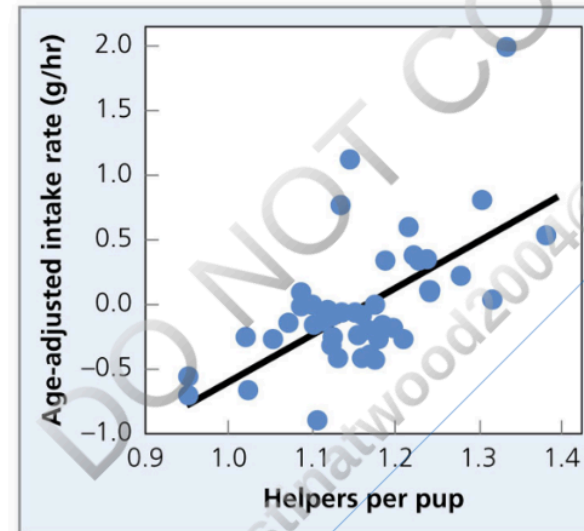
In many social carnivores such as meerkats (*Suricata suricatta*), all adults help protect and feed offspring, even though most of the offspring are produced by a single pair (Figure 16.19). Why? In this species, groups typically contain five to 14 adults and their offspring. The dominant male and female produce about 80% of the pups; thus, subordinates do produce offspring and receive some direct fitness benefits. In addition, a few nonbreeding adults are related to the dominant female and so receive indirect fitness benefits by helping (Clutton-Brock et al. 1999). Finally, there is a positive relationship between a group's size and the foraging success and survival of adults. Therefore, by helping raise offspring, nonbreeding adults also help increase the size of the social group, which yields fitness benefits to themselves, especially compared to attempting to breed on their own in a small group. This last benefit assumes that helpers contribute to the effort to enhance survivorship of pups so that group size will increase. Is that true?



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**FIGURE 16.19. Meerkat helpers.** Adults care for all young in a social group.

Tim Clutton-Brock and his colleagues studied 11 groups of meerkats over five years (Clutton-Brock et al. 2001). Across groups and over time, there was much variation in the number of helpers relative to the number of pups in a group. In each group, the research team quantified the food received by each pup from all group members for three months. They found that as the ratio of helpers per pup increased, so did the average feeding rate and daily weight gain of pups: more helpers meant more food delivered to each pup (Figure 16.20). Those that had higher feeding rates also had higher survival rates. This increase in pup survival can ultimately enhance total group size because pups stay with their natal group for up to three years. In this species, a combination of kin selection (some adults help raise relatives) and ecological constraints (helpers obtain higher feeding rates in larger groups) favors the evolution of cooperative reproduction.



**FIGURE 16.20. Meerkat pup food intake.** As the number of helpers per pup increased, pups had higher food intake. (Source: Clutton-Brock et al. 2001)

## FEATURED RESEARCH Cooperative reproduction in long-tailed tits

Andrew Russell, Ben Hatchwell, and colleagues studied cooperative reproduction and helping behavior in long-tailed tits (*Aegithalos caudatus*) in Great Britain (Figure 16.21) (Russell & Hatchwell 2001; Hatchwell et al. 2004). In spring, monogamous pairs form and begin reproductive behavior (nest building, egg laying, and incubation). However, many nests are destroyed by predators—when that occurs, the nest builders are unlikely to

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incubation). However, many nests are destroyed by predators. When that occurs, the non-breeders are unlikely to have sufficient time to successfully raise offspring in the current breeding season. Many failed breeders become helpers by joining with another pair and feeding their offspring. How might this behavior have evolved?



FIGURE 16.21. Long-tailed tits. A social bird common in Europe.

#### Video: Long-tailed tit chicks being fed

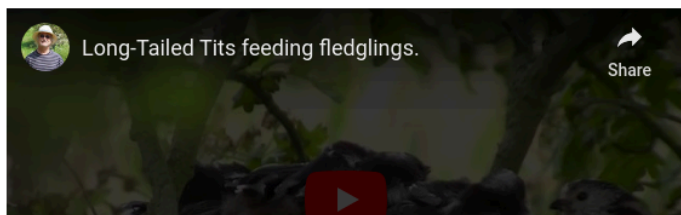
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Video: Long-tailed tit chicks being fed



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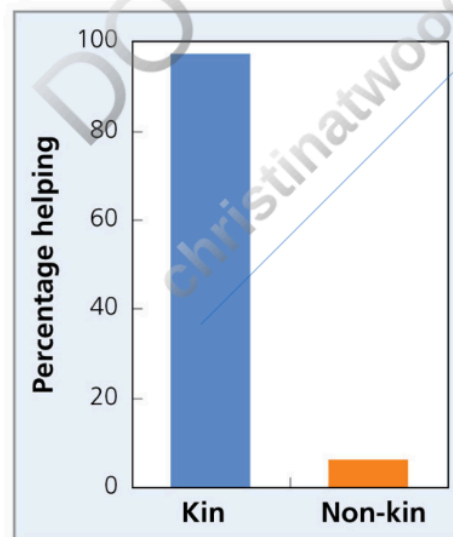
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The team captured and uniquely marked individuals in three populations over the course of several years. They used a combination of known pedigrees and genetic data obtained from blood samples to determine the degree of relatedness among individuals in the study populations. They visited all nests regularly and recorded the success or failure of each, all instances of helping behavior, and the long-term survivorship of nestlings, as determined by recruitment into a social group the following year.

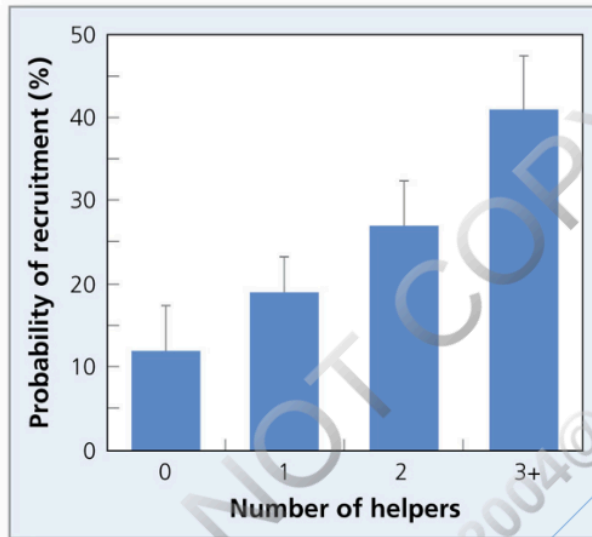
The researchers observed 37 birds they classified as helpers at the nest of a pair. In all cases, these were birds whose own nesting attempt had failed. Nearly all helpers assisted a pair that contained at least one relative: in over 90% of cases, this individual was a close relative, such as a sibling (Figure 16.22). The number of helpers at a nest also positively affected the probability that a nestling would survive and be recruited into the population the following year (Figure 16.23). These data demonstrate that helpers do in fact feed the young of a close relative and do so after their own attempt at reproducing has failed. As such, both kin selection and ecological constraints (lack of time to re-nest after a failed breeding attempt) favor cooperative breeding.



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**FIGURES 16.22. Helping behavior and relatedness in long-tailed tits.** Long-tailed tits helped pairs that contained at least one close relative (kin) more than they helped unrelated pairs (non-kin). (Source: [Russell & Hatchwell 2001](#))



**FIGURE 16.23. Long-tailed tit fledgling success.** Mean (+ SE) probability of recruitment into the adult population as a function of the number of helpers at the nest. The probability of fledgling recruitment into a social group the following year increased with the number of helpers at the nest. (Source: [Hatchwell et al. 2004](#))

## FEATURED RESEARCH Helping behavior in Seychelles warblers

The Seychelles warbler (*Acrocephalus sechellensis*) is another cooperative breeding species with helpers at the nest. Unlike the long-tailed tit, however, helpers in this species are not failed breeders. Instead, they are offspring from previous clutches that have not yet dispersed. Because the helpers are closely related to the parents and offspring they care for, they gain indirect fitness benefits via kin selection. But why do they stay to help instead of attempting to breed on their own?

One possibility is that there are no available territories for them to disperse into. The habitat saturation hypothesis asserts that when few territories are available, a breeding attempt has a low probability of success and likely entails a very high cost in terms of reduced survivorship ([Emlen 1982](#)). Individuals can have higher fitness by staying in an established group to gain the associated fitness benefits of sociality and can also obtain indirect fitness benefits by helping to raise siblings. These individuals are waiting for a better opportunity to breed in the future if territories become available.

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future if territories become available.

Jan Komdeur tested the habitat saturation hypothesis in this species by observing the breeding behavior of translocated Seychelles warblers ([Komdeur et al. 1991](#); [Komdeur 1992](#)). Seychelles warblers were once widely distributed throughout the Seychelles, but due to habitat destruction and the introduction of nonnative species, became a highly threatened single-island endemic species with only 26 individuals on Cousin Island in the 1960s. A conservation management program was introduced and the population grew to over 300 individuals. However, as the population exceeded about 200 individuals, observers began to note the presence of helpers at nest sites, and this behavior eventually became widespread throughout the population. In particular, individuals born in high- and medium-quality territories were highly likely to remain home as helpers. Only individuals born in poor-quality territories were likely to disperse and attempt breeding on their own. These data suggested that habitat saturation was likely occurring on Cousin Island.

Eventually conservationists began to redistribute the species on other islands. This gave Komdeur the opportunity to study the breeding behavior of Seychelles warblers transferred to two islands with abundant suitable habitat to initiate new populations and more directly test the habitat saturation hypothesis. The translocated adults quickly established territories and began to breed. Interestingly, none of the offspring born on the new islands remained at their natal nest to become helpers, and juveniles left at four months of age to begin breeding. In contrast, juveniles on the original island, where population density was high, remained at their natal nest for over 23 months and often became helpers. In this species, the decision by juveniles to stay at their natal nest and help appears to be driven by a lack of breeding opportunities available and kin selection. How juveniles determine the availability of open territories remains to be studied.

In these examples, both kin selection and ecological constraints appear to have played an important role in the evolution of cooperative breeding. Finally, we examine a species in which only ecological constraints appear to favor cooperative reproduction among groups of unrelated individuals.

## FEATURED RESEARCH Social queuing in clownfish

In many permanent groups, individuals exhibit a dominance hierarchy: subordinates do not breed but instead help in defending the group's territory. Over time, as they age and as higher-ranking individuals die, subordinates can move up the social ladder, a process called **social queuing** ([Kokko & Johnstone 1999](#)). Social queuing provides a delayed direct benefit of helping because subordinates can eventually inherit a territory and its breeding opportunities ([McDonald 1993](#); [Field, Shreeves, & Sumner 1999](#); [Kokko & Johnstone 1999](#); [East & Hofer 2001](#)).

Peter Buston studied social queuing in clownfish (*Amphiprion percula*) ([Buston 2004](#)). These social reef fish live in and around sea anemones ([Figure 16.24](#)). Sea anemones are cnidarians: they lack a hard skeleton and possess stinging tentacles that inject a neurotoxin into fish that come into contact with them, an adaptation that is effective in capturing prey. Clownfish have an outer mucus layer that makes them immune to the anemones' sting. As a result, they benefit from the anemones keeping predators at bay.



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**FIGURE 16.24. Clownfish and sea anemones.** Clownfish groups live in association with anemones. Note the size difference among group members.

Clownfish live in small groups that consist of a breeding pair and up to four unrelated nonbreeders. Adults are protandrous: on maturation, they develop into males but later can develop into females. Within each group, there is a size-based dominance hierarchy in which the breeding female is the largest and most dominant fish, followed by the breeding male and then any nonbreeders. Nonbreeders do not have functioning gonads and so obtain no immediate reproductive benefits from group membership, but they often help defend the territory. Why, then, do they stay in a group? Buston predicted that subordinates may obtain future reproductive benefits through social queuing.

To test this idea, he recorded patterns of territory inheritance on three reefs in Papua New Guinea. Over the course of one year, he observed 97 groups and recorded dominance interactions, the recruitment of new individuals, and changes following the disappearance of a breeder. No reversals in rank within the linear dominance hierarchy of groups were observed. Loss of the breeding female always led to a chain reaction: the breeding male changed sex and became the dominant breeding female, and the next-highest-ranking nonbreeder in the group became a sexually mature male. Buston had observed social queuing in action.

Next, he experimentally manipulated 16 groups by removing the breeding male. In each case, nonbreeders moved up the social ladder. The highest-ranking nonbreeder became a sexually mature breeding male, and any new recruit always entered the group as the lowest-ranking member. Buston never observed an outsider usurp a breeding vacancy.

He concluded that nonbreeding group members benefit from group membership by eventually inheriting the territory and thus obtaining reproductive success. Clownfish adults are not strong swimmers and are often preyed upon when they leave their anemones. It is risky to venture out in search of breeding vacancies, away from this protection. This risk may explain why Buston did not observe outsiders taking over a breeding territory. Small

larval recruits join existing breeders and always begin at the bottom of the social queue rather than live alone.

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larval recruits join existing breeders and always begin at the bottom of the social queue rather than live alone. Biding time within a social queue yields higher fitness for an individual, which helps explain why subordinates remain in clownfish groups even though they are unrelated to the breeders and may receive fewer resources and have fewer mating opportunities than dominant individuals.

The examples in this section all involved vertebrates. We now turn our attention to cooperative breeding in invertebrates where we often see the evolution of distinct behavioral and morphological castes, including castes that are sterile—an extreme form of altruism.

## Invertebrate castes

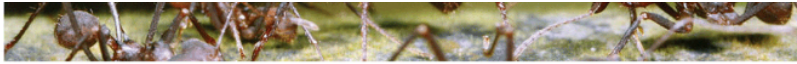
Cooperative breeding occurs in many invertebrates, often in a nest, hive, or colony. Some cooperatively breeding insects, such as paper wasps, are similar to cooperatively breeding vertebrates because all adults are morphologically similar and physiologically capable of reproducing, but some forgo reproduction either to help raise close relatives or to wait in a social queue for a breeding opportunity to arise.

But in other species, we see a new phenomenon, the evolution of **castes**—groups of individuals that engage in distinct behaviors. In some species, castes have evolved particular morphologies associated with their different tasks. For example, morphological and behavioral castes are common in ants. One extreme example can be found in leaf cutter ants in the genus *Atta*. These ants obligately farm a fungus in their subterranean colonies: individuals cut leaves, bring them back to the nest, grow a specialized fungal crop on them, and then consume it. Within a colony, body size of workers can range by almost one order of magnitude and can include over a half dozen castes of workers with distinct morphologies and behaviors ([Wilson 1983a, b](#)). The smallest workers tend the fungal garden, remove refuse, and care for the brood. Medium-sized workers forage for leaves ([Figure 16.25](#)), while the large soldiers both excavate and defend the nest.



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**FIGURE 16.25.** Leaf cutter ant worker. Leaf cutter ant carrying a leaf back to the colony.

## The evolution of sterile castes

In many social invertebrates workers are sterile females: they are physiologically incapable of reproduction. In each colony just one or a few queens reproduce. Workers spend their lives maintaining and defending the nest and helping the queen reproduce. Such **eusocial** species are defined by cooperative care of offspring, reproductive division of labor between breeders and sterile workers, and overlapping generations (Batra 1966; Burda et al. 2000). Eusociality has evolved independently in termites, beetles, aphids, thrips, spiders, and frequently in the insect order Hymenoptera, which includes bees, ants, and wasps.

### Video: A worker, soldier, and reproductive termite

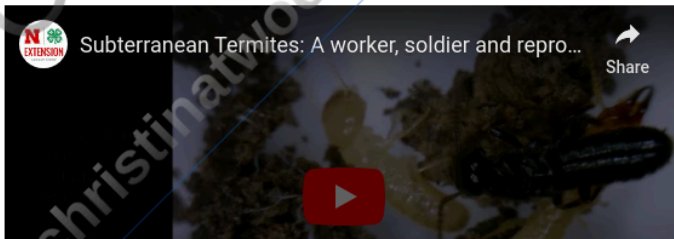
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Video: A worker, soldier, and reproductive termite



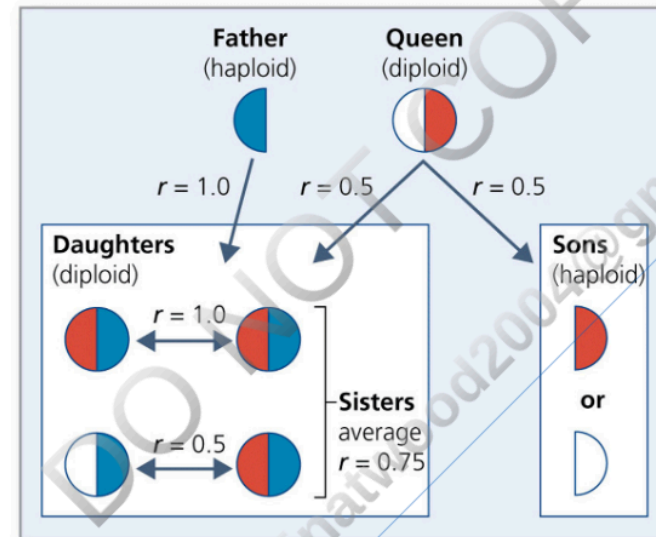
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## Haplodiploidy hypothesis

Darwin (1859) suggested that relatedness among individuals provided the answer to how eusociality can evolve. William Hamilton (1963; 1964) focused on this mechanism to explain why eusociality evolved independently multiple times in the order Hymenoptera, in which sterile workers are typically females. This insect order has an unusual mechanism of sex determination known as haplodiploidy: males develop parthenogenetically from unfertilized eggs and so are haploid, while females develop from fertilized eggs and so are diploid. Due to this **haplodiploid genetic system**, females are more closely related to their full sisters ( $r = 0.75$ ) than to their own daughters ( $r = 0.5$ ) (Figure 16.26).



**FIGURE 16.26.** Haplodiploidy. Daughters share half of their genome with their mother but inherit all of their father's genome. Sons share half of their genome with their mother and none with their father. Sisters share (on average) three-quarters of their genome.

Hamilton suggested that haplodiploidy favors the evolution of sterile daughters because they can achieve higher fitness by helping to raise sisters instead of their own daughters. But this hypothesis cannot be a full explanation for the evolution of sterile workers, because many eusocial species (e.g., termites) have only diploid individuals. In addition, Hamilton ignored the fact that females are related to their full brothers by 0.25 on average, which means they are less closely related to their full brothers than to their own sons ( $r = 0.5$ ). Therefore, for a colony with an equal sex ratio of sons and daughters, the average relatedness among siblings is the same as that between parents and offspring ( $r = 0.5$ ), and so the overall fitness benefits of helping to raise siblings is no higher than that derived from raising offspring (Trivers & Hare 1976; Foster, Wenseleers, & Ratnieks 2006). Because the



haplodiploidy hypothesis fails to explain the repeated evolution of eusociality, researchers began to examine other factors that might better explain this phenomenon.

## Kin selection and ecological constraint hypothesis

The current hypothesis to explain the evolution of sterile workers involves both kin selection and ecological constraints (Alexander 1974; West et al. 2007). With respect to kin selection, all extant eusocial species with sterile castes appear to have descended from ancestor species that exhibited lifetime monogamy, in which a single queen mated with a single male, stored his sperm, and used it for the rest of her life to fertilize her eggs (Hughes et al. 2008). As such, all the offspring she produced were full siblings and were related to one another by the same degree, on average, as parents were to their own offspring; the coefficient of relatedness,  $r$ , would have been 0.5 in both cases (Boomsma 2009). Now consider the behavioral decision faced by potential helpers: leave the natal nest and attempt to produce their own offspring or stay and help to raise siblings. Because the degree of relatedness to their offspring and siblings would have been the same, selection will favor the latter decision when the net fitness benefit of staying to help parents raise siblings is higher than the net benefit of leaving the natal site in an attempt to produce offspring.

The existence of ecological constraints affects the relative benefits and costs of staying to help versus dispersing to breed (Emlen 1982; Heg et al. 2004; Queller & Strassman 1998; Ross et al. 2013). Recall that most eusocial species live and reproduce in a nest, hive, or colony. These sites are vigorously defended from threats by competitive rivals (both conspecifics and heterospecific species), and colonies are best defended by multiple individuals, which means that small incipient colonies are likely to have low fitness because they will be poorly defended. In addition, venturing outside the nest to forage is risky: many workers are killed by predators (Figure 16.27) (e.g., Schmidt-Hempel & Wolf 1988). Finally, there may be few opportunities in an environment to establish a new colony because of habitat saturation. Together, these conditions can result in higher fitness for an individual that forgoes any attempt at reproducing and instead helps to raise close relatives. If these conditions existed for ancestral social insects, they could favor the evolution of eusociality. A recent study of sweat bees has tested this hypothesis.



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**FIGURE 16.27. Eusocial insect worker mortality.** A worker wasp faces high predation risk while away from the colony.

## FEATURED RESEARCH Eusociality in sweat bees

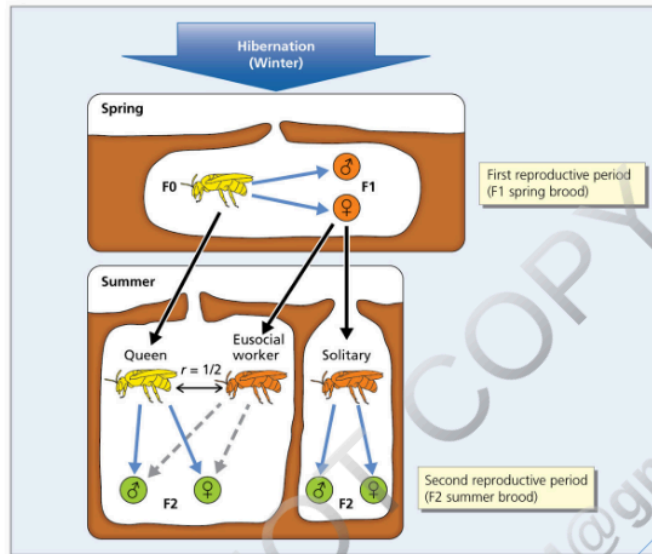
Norihiro Yagi and Eisuke Hasegawa examined how kin selection and ecological constraints play a role in the evolution of sterile workers in the sweat bee, *Lasioglossum baleicum* (Yagi & Hasegawa 2012) (Figure 16.28). In this species, two broods are produced each year (Figure 16.29). Adult females that overwinter (defined as generation F0) produce the first brood, F1 individuals, in the early spring. Later in the summer, after the F1 generation has matured and mated, the females in both groups (F0 and F1) produce a second brood, the F2 generation. Within a population, there is much variation in the social organization of nests during this second reproductive period. In most nests, some F1 females stay to help their F0 mother produce offspring. These F1 females are sterile, and so these nests are eusocial (eusocial, multiple-female nests). All other F1 females are fertile and some nest as solitary individuals (single female nests), while others join the nest of an unrelated female and produce their own offspring (not eusocial, multiple female nests).



**FIGURE 16.28. Sweat bee, *Lasioglossum* individual feeding on a flower.**

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**FIGURE 16.28.** Sweat bee, *Lasioglossum* individual feeding on a flower.

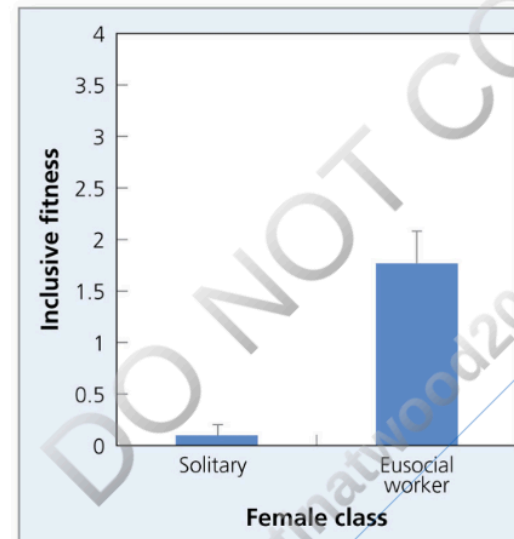


**FIGURE 16.29.** Yearly reproduction in sweat bees. F0 females (yellow) produce F1 offspring (orange) in spring. Some F1 daughters remain to help their mother produce a second brood in summer—these daughters are sterile (eusocial workers) and only gain indirect fitness (gray dashed lines) by helping their mother raise F2 siblings. Other F1 daughters nest as solitary females and produce F2 offspring. (Source: Yagi & Hasegawa 2012)

Yagi and Hasegawa examined 33 nests in Japan over two years to calculate the social structure present and the fitness of the F1 females that nested either alone or in multiple-female nests. Nests are constructed underground and contain several larval cells, with each containing a single egg and food for the larvae. In each nest, all adults were marked to determine the number of females. At the end of the summer, the nests were excavated to determine the fate of the F2 larval cells (successfully pupated individual or empty cell). Offspring and adults from each nest were then genotyped using microsatellite DNA analysis to determine kinship relationships. This allowed calculation of the inclusive fitness of each F1 female in a nest, based on the number of F2 pupae successfully produced and weighted by their degree of relatedness to each adult.

In both solitary and multiple-female nests, an average of four larval cells were produced per female, so the number of females in a nest did not affect individual female reproductive potential. However, the calculated inclusive fitness of sterile worker females was significantly higher than that of solitary females (Figure 16.30), showing that selection favors individuals that do not reproduce directly, but instead stay to help a relative reproduce, as outlined by Hamilton's rule.

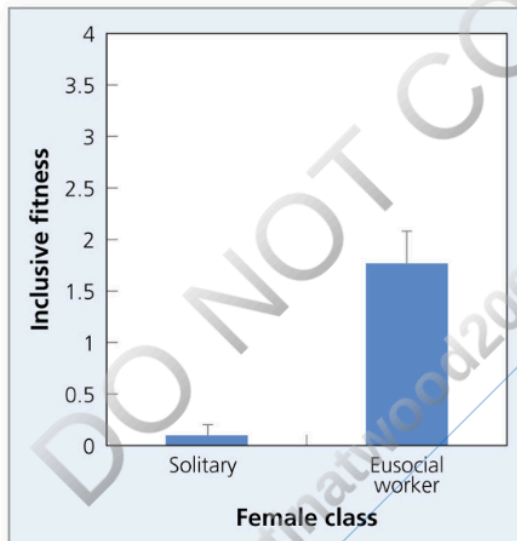
Why was fitness so low for solitary females? Nests with a single female had significantly lower larval survival than nests with multiple nesting females. The research team suggested this likely occurred because multiple females are more effective defenders against predation by ants. As such, predation risk by ants is an ecological constraint that renders low fitness to solitary nesters and so reduces the cost of altruism in this species, and thus favors the evolution of sterile workers. Further work is needed to understand the development of sterility in eusocial females and why solitary nesting females exist in the population, given their low fitness.



**FIGURE 16.30.** Worker fitness. Mean (+ SE) inclusive fitness of solitary and sterile eusocial workers. (Source: Yagi & Hasegawa 2012)

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**FIGURE 16.30. Worker fitness.** Mean (+ SE) inclusive fitness of solitary and sterile eusocial workers. (Source: Yagi & Hasegawa 2012)

## CHAPTER REVIEW

### 16.1 Inclusive fitness theory explains the evolution of cooperation among related individuals

- Hamilton's rule, or kin selection, predicts when cooperation will evolve.
- Kin selection explains why adult female ground squirrels give alarm calls more often than adult males or juveniles do.
- Male turkeys in coalitions with closely related males have higher fitness than solo males.

### 16.2 Individuals can discriminate kin from non-kin

- Sticklebacks use direct familiarization based on previous association to identify kin when selecting shoalmates.
- Cockroaches use indirect familiarization based on CHC profiles to identify kin when selecting social partners.

### 16.3 Cooperative behavior among unrelated individuals involves byproduct mutualisms or reciprocity

- Byproduct mutualisms are behaviors that enhance the fitness of an individual actor and others.
- Direct reciprocity involves a costly behavior from which an actor can benefit if the recipient of an altruistic act reciprocates in the future.
- The prisoner's dilemma describes how cooperation via direct reciprocity is subject to cheating. The ESS is the tit-for-tat strategy.
- Vampire bats are more likely to share food if prior food has been received from the recipient in the past, exemplifying direct reciprocity.
- Japanese macaques groom each other based on prior interactions rather than kinship, exemplifying reciprocal altruism.
- Red-winged blackbirds cooperate in nest defense with unrelated neighbors as described by the tit-for-tat strategy.
- The snowdrift game describes a scenario that can often favor the evolution of cooperation. The ESS is a mixed strategy in which individuals



exhibit cooperative behavior.

- During migration, bald ibis cooperate by alternatively leading and following when flying, in a manner consistent with the snowdrift game.
- Cooperation among unrelated individuals can also evolve through indirect reciprocity, in which an individual learns about and then helps others that have high altruistic tendencies.
- In cleaner fish–client fish interactions, client fish cooperate with individual cleaners only after learning about their altruistic tendencies.
- Chimpanzees and orangutans can learn about the altruistic tendencies of humans.

#### 16.4 Kinship and ecological constraints favor cooperative reproduction

- In cooperative breeding species, some adults do not reproduce but help to raise the offspring of others.
- Kin selection and ecological constraints explain how individuals can benefit by helping to raise others' offspring whereas haplodiploidy cannot.
- In meerkats, both kin selection and ecological constraints favor the evolution of cooperative reproductive behavior.
- Long-tailed tit helpers are failed breeders that do not have sufficient time to re-nest and are related to the breeding pair.
- Seychelles warbler helpers are previous year's offspring that lack breeding opportunities and so stay in their natal nests to help kin.
- Clownfish subordinates help unrelated offspring by defending a territory and can eventually inherit the territory and its breeding opportunities.
- Some cooperative breeding invertebrates have evolved distinct morphological castes, and individuals specialize on different tasks.
- In eusocial species, one caste reproduces, while all others are sterile workers. Kin selection and ecological constraints can explain the evolution of sterile castes.

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- Direct reciprocity involves a costly behavior from which an actor can benefit if the recipient of an altruistic act reciprocates in the future.
- The prisoner's dilemma describes how cooperation via direct reciprocity is subject to cheating. The ESS is the tit-for-tat strategy.
- Vampire bats are more likely to share food if prior food has been received from the recipient in the past, exemplifying direct reciprocity.
- Japanese macaques groom each other based on prior interactions rather than kinship, exemplifying reciprocal altruism.
- Red-winged blackbirds cooperate in nest defense with unrelated neighbors as described by the tit-for-tat strategy.
- The snowdrift game describes a scenario that can often favor the evolution of cooperation. The ESS is a mixed strategy in which individuals

exhibit cooperative behavior.

- During migration, bald ibis cooperate by alternatively leading and following when flying, in a manner consistent with the snowdrift game.
- Cooperation among unrelated individuals can also evolve through indirect reciprocity, in which an individual learns about and then helps others that have high altruistic tendencies.
- In cleaner fish–client fish interactions, client fish cooperate with individual cleaners only after learning about their altruistic tendencies.
- Chimpanzees and orangutans can learn about the altruistic tendencies of humans.

#### 16.4 Kinship and ecological constraints favor cooperative reproduction

- In cooperative breeding species, some adults do not reproduce but help to raise the offspring of others.
- Kin selection and ecological constraints explain how individuals can benefit by helping to raise others' offspring whereas haplodiploidy cannot.
- In meerkats, both kin selection and ecological constraints favor the evolution of cooperative reproductive behavior.
- Long-tailed tit helpers are failed breeders that do not have sufficient time to re-nest and are related to the breeding pair.
- Seychelles warbler helpers are previous year's offspring that lack breeding opportunities and so stay in their natal nests to help kin.
- Clownfish subordinates help unrelated offspring by defending a territory and can eventually inherit the territory and its breeding opportunities.
- Some cooperative breeding invertebrates have evolved distinct morphological castes, and individuals specialize on different tasks.
- In eusocial species, one caste reproduces, while all others are sterile workers. Kin selection and ecological constraints can explain the evolution of sterile castes.

## CHAPTER REVIEW

### 16.1 Inclusive fitness theory explains the evolution of cooperation among related individuals

- Hamilton's rule, or kin selection, predicts when cooperation will evolve.
- Kin selection explains why adult female ground squirrels give alarm calls more often than adult males or juveniles do.
- Male turkeys in coalitions with closely related males have higher fitness than solo males.

### 16.2 Individuals can discriminate kin from non-kin

- Sticklebacks use direct familiarization based on previous association to identify kin when selecting shoalmates.
- Cockroaches use indirect familiarization based on CHC profiles to identify kin when selecting social partners.

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# Glossary

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**adaptation** A trait that enhances fitness (survivorship and reproduction). Also, an evolutionary process that results in a population of individuals with traits best suited to the current environment.

**additive effects (A)** The average effect of individual alleles on the phenotype.

**aggressive mimicry** A situation in which a predator mimics a nonthreatening model.

**alarm call** A unique vocalization produced by social animals when a predator is nearby.

**alarm signal hypothesis** The hypothesis that advertisement behavior functions to warn nearby conspecifics of danger.

**Allee effect** A situation in which the fitness of individuals increases with increased population density.

**alogrooming** The grooming by one individual of another to remove ectoparasites.

**alternate hypothesis ( $H_a$ )** The statistical hypothesis that the proposed explanation for an observation does significantly affect the behavior of the organism.

**alternative reproductive tactics** The existence of multiple behavioral mating phenotypes in a population.

**altruism** A behavior that results in the increased fitness of another individual and involves a cost to the individual performing the behavior. Also known as helping behavior.

**ancestral trait** A trait found in the common ancestor of two or more species. Also called a **plesiomorphic trait**.

**animal behavior** Any internally coordinated, externally visible pattern of activity that responds to changing external or internal conditions.

**animal culture** Differences in multiple traditions among populations.

**anisogamy** The existence of differently sized gametes (small and large) in the different sexes.

**anthropomorphism** The attribution of human motivations, characteristics, or emotions to animals.

**apomorphic trait** A trait found in an organism that was not present in the last common ancestor of a group of two or more species. Also known as a **derived trait**.

**aposematic coloration** Brightly colored morphology in a species that stands out from the environment and is associated with noxious chemicals or poisons that make individuals unpalatable or dangerous prey.

**audience effect** The presence of a bystander influences the behavior of a signaler.

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**audience effect** The presence of a bystander influences the behavior of a signaler.

**bar graph** A graph that represents categorical data in rectangular bars arranged horizontally or vertically.

**Bateman's hypothesis** The hypothesis that female reproductive success is most strongly limited by the number and success of eggs that a female can produce, while male reproductive success is limited by the number of mates a male has.

**Batesian mimicry** The resemblance of a palatable mimic to an unpalatable model that predators have learned to avoid.

**behavioral traditions** Differences in behavior among populations that are transmitted between generations through social learning.

**bicoordinate navigation** The ability to identify a geographic location using two varying environmental gradients.

**biparental care** Both parents provide care for offspring.

**breeding dispersal** The abandonment of one breeding site to move to another.

**brood parasitism** A behavior in which a female (brood parasite) lays an egg in the nest of another female.

**brood reduction** The death of some siblings as a result of reduced parental care to enhance the fitness of surviving siblings.

**byproduct mutualism** When an individual's behavior enhances both its own fitness and the fitness of others.

**bystander** A third-party individual that detects a signal transmitted between a signaler and a receiver. Also called an **eavesdropper**.

**cache** Food stored in a hidden location for later retrieval.

**castes** Morphologically and behaviorally distinct individuals within a social group.

**challenge hypothesis** The hypothesis that male–male interactions increase plasma testosterone and thus sustain subsequent aggressive behavior.

**chemoreception** The process by which an animal detects chemical stimuli.

**classical conditioning** A type of learning in which a novel stimulus is paired with an existing stimulus and elicits a particular innate response. Eventually the novel stimulus alone elicits the same response as the existing stimulus. Also called **Pavlovian conditioning**.

**cleaner fish** Fish that feed on ectoparasites and the dead skin of other fish.

## CHAPTER 15

# Sociality

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
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### Concepts

- 15.1 [Sociality can evolve when the fitness advantages of close associations exceed the costs](#)
- 15.2 [Dominance hierarchies reduce the social costs of aggression](#)
- 15.3 [Ecology and phylogeny influence the evolution of sociality](#)
- 15.4 [Hormones regulate social behavior](#)

### Features

- |                        |  |
|------------------------|--|
| Scientific Process     | 15.1 <a href="#">Mesotocin and sociality in zebra finches</a>  |
| Applying the Concepts  | 15.1 <a href="#">Group aerodynamic advantages in cyclists</a>  |
|                        | 15.2 <a href="#">Group size of social species in captivity</a> |
| Quantitative Reasoning | 15.1 <a href="#">Benefits of group foraging</a>                |

We love snorkeling and scuba diving because they let us be part of a whole different, exciting ecosystem. We've been fortunate enough to explore Belize's barrier reef, which is one of the largest in the world. Day and night, we donned our masks and fins and explored different sections of the reef. We saw an amazing diversity of corals, beautiful urchins, and even lobsters and sea turtles, but most remarkable was the abundance and diversity of colorful fishes. One striking aspect of the fish was the evident variation in the group sizes of different species. For instance, we always saw just a single green moray eel (*Gymnothorax funebris*) peering out of its rocky crevice. The four-eyed butterfly fish (*Chaetodon capistratus*) foraging over the shallow reef were in small groups of no more than a dozen individuals, but blue striped grunt (*Haemulon sciurus*) (Figure 15.1) were in groups of several dozen or even up to a thousand.

Understanding and explaining this variation in social behavior are the goals of this chapter. We will examine many aspects of group living, beginning with a discussion of the benefits and costs of life in groups to better understand variation in group size among species. We then focus on a behavior that reduces one such cost—the formation of dominance hierarchies. We also explore factors thought to be important for the evolution of social living in many groups, and conclude by examining how hormones regulate social behavior.



FIGURE 15.1. Sociality. A school of blue striped grunts (*Haemulon sciurus*).

### Video: Blue striped grunt fish

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## 15.1 Sociality can evolve when the fitness advantages of close associations exceed the costs

### Learning Objectives

After reading this section, you should be able to

- describe the benefits and costs associated with living in social groups and
- predict when sociality should evolve examining the benefits and costs.

Flocks of birds, schools of fish, swarms of insects, and herds of mammals are examples of social groups—sets of individuals that remain in close proximity and interact with one another. As we mentioned, there is tremendous variation across species in the size, composition, and persistence of social groups—that is, their degree of **sociality**. Group composition can also differ with respect to sex and age. During the nonreproductive season, for instance, many ungulates (hoofed animals) such as caribou (*Rangifer tarandus*) form single-sex groups, and flocks of common ravens (*Corvus corax*) are often composed of a single age class, juveniles. The time that individuals spend in groups can vary seasonally or daily. For example, European starlings (*Sturnus vulgaris*) tend to join large flocks in the fall and winter and then live as pairs defending their territories during the breeding season. In contrast, many primates, parrots, ants, wasps, and coral reef fish spend their entire lives in a social group. How can we explain all this variation?

Sociality can evolve only if it results in an individual in a group obtaining higher fitness than it would by living alone. In other words, the benefits of sociality for an individual must be greater than the costs. Numerous potential benefits and costs of sociality have been identified (e.g., [Hoogland & Sherman 1976](#); [Krause & Ruxton 2002](#)). Benefits can include reduced search time to find resources (food or mates), increased feeding success as a result of cooperative hunting, enhanced ability to defend a resource, reduced predation risk, lower physiological costs of thermoregulation and movement ([Figure 15.2](#)), division of labor (task specialization), and communal care of young. Costs associated with sociality can involve increased aggression and competition for resources, enhanced predator attraction and disease transmission, and, in some species, infanticide and cannibalism ([Table 15.1](#) summarizes benefits and costs). We have already discussed social behavior in regard to learning ([Chapter 7](#)), antipredator behavior ([Chapter 9](#)), and aggression ([Chapter 11](#)). Here, we examine some additional aspects of group life.





**FIGURE 15.2.** Physiological benefits of sociality. Bats huddle to minimize heat loss.

**TABLE 15.1** Some benefits and costs of sociality.

Benefits	Costs
Decreased time to find food	Increased aggression
Enhanced foraging success	Increased competition
Enhanced resource defense	Increased attraction to predators
Decreased predation risk	Increased disease transmission
Reduced costs of thermoregulation	Increased infanticide
Specialization and division of labor	Increased cannibalism
Communal care of young	
More rapid learning	
Reduced cost of movement	

## FEATURED RESEARCH Reduced search times for food

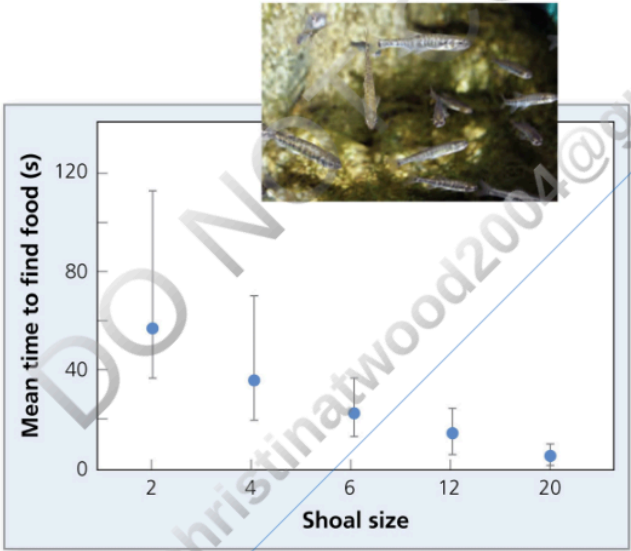
Food is often inconspicuous in the environment, and so animals spend considerable time searching for it. How might sociality increase foraging success? Some birds have higher encounter rates with insects when group member movements can flush prey out of hiding (Harsha et al. 2007). In other cases, groups can find food patches faster because more individuals engage in searching. Once hidden food is found, all group members can move to the patch to feed.

Tony Pitcher, Ann Magurran, and Ian Winfield investigated this benefit of sociality in the common minnow

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(*Phoxinus phoxinus*), a small fish found throughout Europe in freshwater streams and rivers. Minnows feed on a variety of food items buried in the gravel or sand, including mollusks, insects, and crustaceans. The team tested the prediction that as group size increases, the search time for an individual to find hidden food decreases (Pitcher, Magurran, & Winfield 1982). They conducted experiments in a large aquarium (2 m × 70 cm × 70 cm) that held schools of two to 20 fish. To examine the effect of group size on an individual's time to find food, the researchers uniquely marked one fish (the test fish) and recorded its behavior. Before the start of a trial, they placed a food patch consisting of 84 ice cube tray wells filled with gravel in the aquarium. Dried fish protein flakes were randomly added to one of the cubes. The researchers then placed the group in the tank and recorded the amount of time until the test fish found the food. They conducted four replicates of this experiment, using a different test fish, for each school size.

As predicted, the time before the test fish found the food declined as group size increased (Figure 15.3). This finding demonstrates one advantage of group living: the larger the group, the less time it takes an individual to find food because others are searching for it as well.



**FIGURE 15.3.** Time to find food. Mean ( $\pm$  SE) time to find food. Individual minnows find food faster when they feed in shoals of larger sizes. (Source: Pitcher, Magurran, & Winfield 1982). Inset: minnow.

## Foraging benefit: Information about distant food locations

An individual minnow in a school is alerted to the presence of food by seeing a nearby conspecific feeding. Can individuals also learn about more distant food sources from others? Roi Harel, Orr Spiegel, Wayne Getz, and Ran Nathan examined whether groups of communal roosting Eurasian griffon vultures (*Gyps fulvus*) (Figure 15.4)

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could be a source of information about distant food sources (Harel et al. 2017). Vultures are obligate scavengers that feed on large carcasses that can persist for several days. Individuals roost in large social groups at night. The researchers tested the information center hypothesis (ICH), which states that individuals can benefit from living in groups, such as communal roosts, by gaining information about distant ephemeral food sources from other group members.



**FIGURE 15.4. Eurasian griffon vultures.** Griffon vultures are a communal species that roost together at night.

Harel and his colleagues studied a population of approximately 200 individuals in a large area (25,000 km<sup>2</sup>) managed by the Israel Nature and Park Authority, which randomly deploys carcasses at several locations throughout the area. They fitted dozens of individuals with GPS tags that allow for tracking. To test the ICH, the team needed to identify an individual's information status at the start of a day when it left the roost. Because vultures detect carcasses at a distance of up to 4 km, an "informed" individual was defined as one who had flown within 2 km of a feeding station in the preceding two days; many had fed on a carcass. "Uninformed" individuals had not been within 10 km of a carcass in the preceding two days.

#### Video: Tagged griffon vultures feeding on carcasses

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Video: Tagged griffon vultures feeding on carcasses

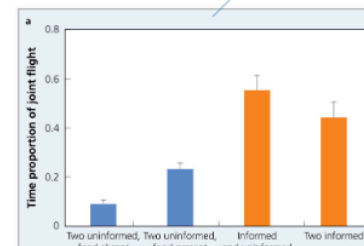
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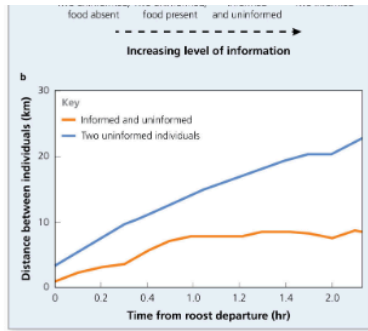
The researchers focused on dyads (pairs) of vultures that departed a roost synchronously. The ICH predicts that in pairs with an informed individual, the uninformed individual will follow it to the carcass: in these dyads, individuals should remain relatively close together (within visual contact of 4 km) and the informed one will be in the leading position (closer to the carcass during the flight).

The team followed 76 vultures at over 45 roosts and collected approximately 30,000 daily trackings. They noted that while the vultures' departure from the roost was highly synchronized, dyads differed in their behavior. Dyads with at least one informed individual spent significantly more time in joint flight (< 4 km apart) and on average were closer together while flying than pairs with two uninformed individuals (Figure 15.5). Furthermore, informed individuals tended to fly ahead of the uninformed individual, especially at the beginning and end of the flight to the carcass.



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**FIGURE 15.5. Vulture dyad behavior.** Dyads with at least one informed individual (a) spent more time together (blue bars indicate uninformed pairs and orange bars indicate at least one informed individual) and (b) stayed closer together than dyads with two uninformed individuals (blue line indicates uninformed pair and orange line indicates one informed individual). (Source: [Harel et al. 2017](#))

These data indicate that one benefit of social roosting may be to obtain information about distant food sources as articulated in the ICH. This may be a substantial benefit for vultures, given that their food rapidly decays or is consumed by others and that a carcass is often more than enough food for all individuals in an area. However, questions still remain, such as how unsuccessful individuals identify successful individuals at the roost. The authors suggest that visual signs such as bloodied feathers or a full crop might provide such information, but further study is required.

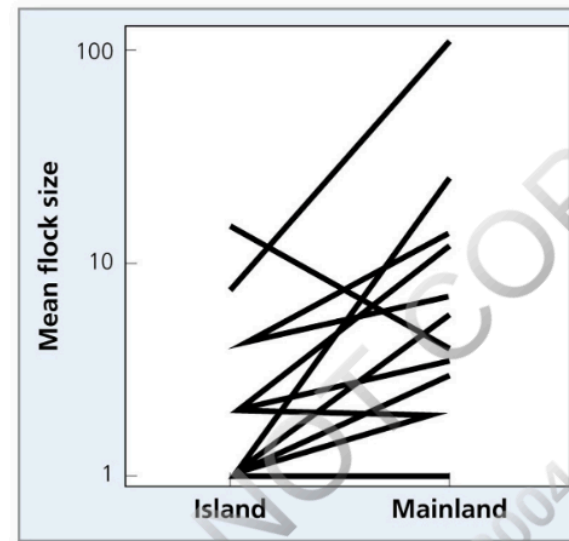
## FEATURED RESEARCH Antipredator benefit of sociality in birds

A second benefit of sociality involves predation risk. As we saw in [Chapter 9](#), individuals in groups spot approaching predators sooner than solitary individuals and so can have more time to take evasive action. In addition, individuals in groups spend less time being vigilant, which frees up more time for other activities such as feeding.

If individuals associate with others to obtain such antipredator benefits, one can predict that variation in predation risk should explain variation in group size. [Guy Beauchamp \(2004\)](#) used the comparative approach to test this prediction by examining data on flocking behavior—the typical size of flocks—in matched pairs of island and closely related mainland species of birds. To test the prediction, he searched the literature for islands where predation on flocking bird species in the nonbreeding season was deemed to be negligible because predators were absent or did not co-occur with a focal species. For these islands, he collected data on flocking behavior of each species and then matched each island species with a closely related mainland pair, often the same species or subspecies or a closely related sister species based on published phylogenetic analyses. Finally, he characterized the flocking behavior of each mainland species pair.

Beauchamp's analysis identified 22 island and 23 mainland species. He found that flocking behavior differed significantly between the species pairs: both mean and maximum flock size were smaller in the island species

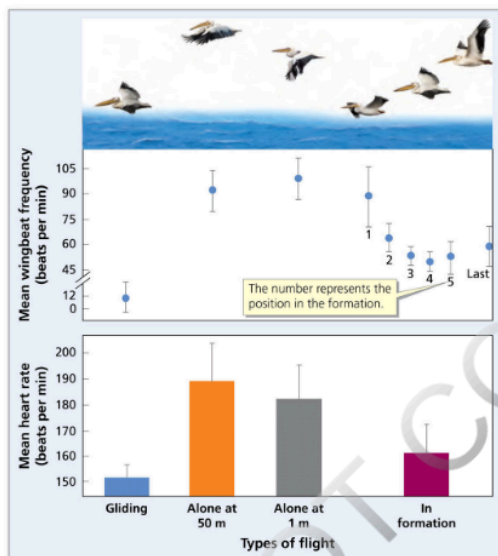
significantly between the species pairs. Both mean and maximum flock size were smaller in the island species ([Figure 15.6](#)). Subsequent analyses indicated no significant difference in body mass, habitat use, or diet for these species pairs. Thus, these data support the hypothesis that predators are an important factor that promotes social aggregations in many bird species.



**FIGURE 15.6. Flock sizes.** Comparison of mean flock size for species pairs on the island and mainland. Each line connects a species pair. For most species pairs, flock sizes were larger on the mainland. (Source: [Beauchamp 2004](#))

## Movement benefits: efficient aerodynamics and hydrodynamics

Another hypothesized benefit of sociality is an aerodynamic or hydrodynamic advantage of moving within a group through air or water, respectively. For example, many large birds such as geese and cranes fly in a V-formation, with fairly uniform spacing between individuals. Do they obtain an aerodynamic benefit that reduces the cost of flying? Henri Weimerskirch and colleagues examined this question using trained white pelicans (*Pelecanus onocrotalus*) ([Weimerskirch et al. 2001](#)). These researchers placed heart rate monitors on the birds and videotaped their flight formations as they followed a motorboat or ultralight airplane. Birds flying in a V-formation had a lower wing-beat frequency and heart rate than birds flying alone, probably because they were flying in the wake of another bird ([Figure 15.7](#)). These data demonstrate a clear decrease in energy expenditure for birds flying in formation. Interestingly, smaller species like sparrows do not fly in formation, perhaps because their body size does not allow the same aerodynamic advantage, although this idea has not been formally tested ([Hummel 1995](#)).



**FIGURE 15.7. Flying effort in pelicans.** Pelicans flying in a V-formation had lower mean ( $\pm$  SE) wing-beat frequency (top) and heart rate (bottom) than birds flying alone. (Source: Weimerskirch et al. 2001)

#### Video: Pelicans flying in formation

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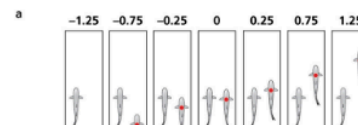
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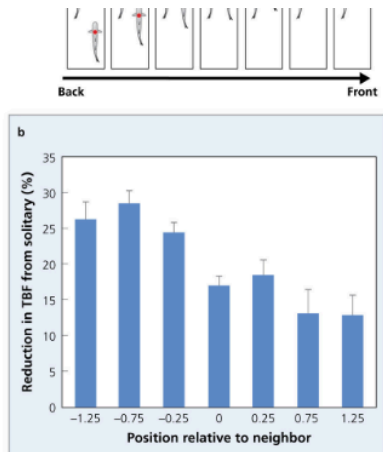
## FEATURED RESEARCH Hydrodynamics in schools of juvenile gray mullet

In a similar manner, many fish and marine mammals swim in coordinated fashion. The propulsive jet of water produced by a beating fish tail or mammalian fin creates small vortices that can reduce drag for others swimming in the immediate wake (Alexander 2004). Recent theoretical work suggests that flow dynamics might also provide hydrodynamic benefits when swimming next to, and perhaps even in front of, other individuals (Hemelrijk et al. 2014).

Stefano Marras and his colleagues examined whether fish in any position in a group have a reduced cost of swimming compared to solitary individuals (Marras et al. 2015). They examined the hydrodynamics of schools of juvenile gray mullet (*Liza aurata*), a common schooling fish in the Atlantic Ocean. The research team created a swimming tunnel in which they recorded the behavior of individually marked focal fish swimming at a constant speed either alone or in a school of eight fish. The fish were videotaped swimming for 20 minutes at 10, 20, and 30 cm per second. During this time the focal individual's tail-beat frequency (an index of energetic cost) was recorded while it swam in each of seven different positions, ranging from the front to the back of the group (Figure 15.8a).

For all group positions, individuals exhibited lower tail-beat frequencies when swimming in groups compared to swimming alone (Figure 15.8b). This occurred for all three swim speeds, with fish swimming at the slowest speeds showing the greatest reduction in overall tail-beat frequency. Using oxygen uptake data estimates from previous research (Killen et al. 2012), Marras and colleagues estimated a 10% to 20% reduction in energetic costs. They found that the further back the focal fish from its nearest neighbor, the more energy it saved. Somewhat surprisingly, even fish in the front of the school had a reduction in tail-beat frequency compared to fish swimming alone. Moving objects create a zone of high pressure in front of them, which can reduce hydrodynamic and aerodynamic drag for group leaders, reducing the cost of movement relative to moving through the environment alone (Applying the Concepts 15.1). This study indicates that the aerodynamic and hydrodynamic benefits of group living may be even more widespread than previously thought.





**FIGURE 15.8. Hydrodynamic benefit in juvenile gray mullet.** (a) Red dots indicate the position of the focal fish relative to its nearest neighbor. Negative values indicate focal fish swimming behind its nearest neighbor. (b) The mean (+ SE) reduction in tail-beat frequency (TBF) of focal fish swimming in different positions as compared to swimming alone. (Source: [Marras et al. 2015](#))

#### Video: School of marked mullet in swimming tunnel at three different speeds

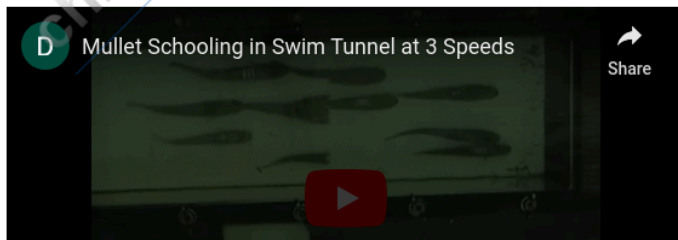
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#### APPLYING THE CONCEPTS 15.1

##### Group aerodynamic advantages in cyclists

Can [Marras et al.'s \(2015\)](#) findings be applied to elite cyclists? Nathan Barry and his colleagues examined aerodynamic drag on individual elite cyclists riding alone or as a team of four in a large wind tunnel ([Barry et al. 2015](#)). The bicycles were mounted on a rig that standardized the distance between bicycles at 120 mm. Each rider was tested alone and at each of the four positions in the line; all tests were conducted at a wind speed of 65 km/h, the approximate speed of an elite men's pursuit team. Compared to when riding alone, individuals experienced an average of 5%, 45%, 55%, and 57% less drag when in positions 1, 2, 3, and 4, respectively. This means that even individuals in the front experience less drag than when riding alone.

The researchers also examined the effect of different riding postures (head up, head down, elbows in) at each position. The head-raised posture increased drag in all four positions whereas head down decreased drag in varying amounts. The elbows-together posture both decreased drag at the front and end rider positions and increased drag for riders in the middle. These results indicate riding in a group is advantageous for all riders in all positions and the changing body posture of one rider can influence the drag on another. Given that milliseconds can separate winners and losers, these results can help riders determine the best aerodynamic positions for a race. ■

#### FEATURED RESEARCH Social heterosis in ants

Individuals living in relatively stable groups can also benefit when group members specialize on different tasks. Such specialization allows an individual to perform a task more efficiently, which then benefits all group members, including that individual. For example, some might specialize on bringing food back to the group, while others focus on caring for offspring or aggressive defense of a group resource such as a territory. This division of labor among group members ([Ydenberg & Hemerik 2016](#)) has been called the skill pool effect ([Giraldeau 1984](#)).

Does this effect result in higher fitness for individuals living in groups? Ants live in colonies with dozens to thousands of workers who perform a variety of tasks. Andreas Modlmeier, Julia Liebmann, and Susanne Foitzik tested the prediction that behavioral specialization among workers within a colony enhances fitness in the ant *Temnothorax longispinosus* ([Modlmeier et al. 2012](#)), a species that lives in small colonies (of about 40 workers) in deciduous forests in northeast North America. All workers in this species forage, aggressively defend the nest, and care for offspring, but individuals differ in their propensity to engage in these different tasks; that is, they exhibit a

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division of labor.

To determine how division of labor affects colony fitness, the research team first needed to characterize behavioral variation within each colony; they needed to determine how similar or different individuals behave. The researchers collected ant colonies from the wild and kept them under identical conditions in the lab. They tested ten randomly selected workers per colony and used the mean and standard deviation from these tests as a measure of colony behavior and its variation. They examined brood care, exploration of novel environments, and aggression. To study brood care behavior, they placed each worker in an arena with a worker pupa and measured the frequency of pupa grooming. For exploration of novel objects, they placed single ants in an apparatus with eight chambers that each contained an unfamiliar chemically distinct object, such as dried pieces of oregano, thyme, or rosemary, and measured how often each worker's antennae explored each object. They quantified aggression by placing each worker in a small arena with a dead non-nestmate and recorded all aggressive interactions such as biting, dragging, and stinging every 20 seconds for five minutes. Colony fitness was estimated as per capita productivity over a nine-month period, calculated as the total mass of brood in the nest (offspring weight) divided by the total number of workers.

Modlmeier and colleagues found much variability in the degree of worker specialization among colonies. Interestingly, colonies with more behavioral specialization with respect to brood care and exploration of novel objects had higher productivity, as predicted by the division of labor hypothesis. Perhaps colonies with higher behavioral specialization are able to react more quickly to changes in conditions such as a threat to the nest or the discovery of a new food source compared to colonies with less behavioral specialization (Myerscough & Oldroyd 2004). The researchers did not find the same relationship between behavioral specialization in aggressive behavior and colony productivity. They propose that this might be because laboratory colonies do not have to defend their nest or compete for resources in the way that colonies in the wild do.

## The costs of sociality

Given the many benefits of sociality, why don't all individuals live in social groups? The answer is that sociality also entails costs: individuals in groups are surrounded by close competitors. Competition, when individuals negatively affect one another, can be intense in groups of conspecifics because individuals require the same resources for survival and reproduction. For example, when a group of minnows finds a food patch, all of them exploit the food. If the food is limited, each individual obtains less than it would if it fed alone, and its fitness, in terms of energy consumed, is reduced. As group size increases, so does the level of competition and the frequency of aggressive interactions. Therefore, competition for resources will often be keen and is considered a primary factor that limits the size of groups. In addition, diseases are more readily transmitted among individuals that live in groups, and so individual fitness can decline as group size increases. Let's see how researchers study these costs of group living.

## FEATURED RESEARCH Group size and food competition in red colobus and red-tailed guenons

If competition for resources often limits group size, we can predict that low-resource environments should have

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smaller group sizes than high-resource environments. In other words, we can predict that there should be a positive correlation between the resources in a habitat and observed group size. Colin and Lauren Chapman tested this prediction in two species of primates in Uganda: red colobus (*Procolobus pennantii*) and red-tailed guenons (*Cercopithecus ascanius*) (Chapman & Chapman 2000). These primates live in tropical forests in equatorial Africa; group size ranges from fewer than ten to several dozen individuals. Both species feed on a variety of fruits and vegetation.

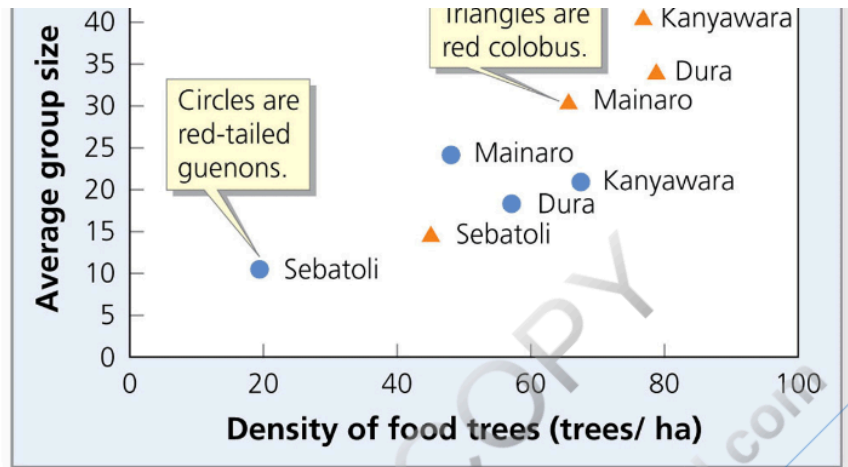
The Chapmans studied the two species at four sites in Kibale National Park over a period of two years (Figure 15.9). To examine the influence of competition for resources on sociality, they first characterized the monkeys' specific diets at each site. Both species fed primarily on young leaves, leaf buds, fruits, and flowers from dozens of tree species. Because all food items came from trees, the researchers could estimate food abundance at each site from the density of food trees, the presence of fruits or flowers, and the stage of leaf development. They established four to six 200 m paths, or transects, across each site. Each month, they walked along the transects to examine each potential food tree and to determine whether it offered food for the monkeys. Food trees were identified as those in which a species spent greater than 10% of its foraging time. They also observed the size of all groups at each site for each species.



**FIGURE 15.9.** Red colobus and red-tailed guenon. (a) Red colobus and (b) red-tailed guenons feed in groups.

The Chapmans found a positive relationship between the density of food trees and average group size across the four sites, as predicted (Figure 15.10). This finding supports the hypothesis that group size is limited by competition for food. Because the monkeys' sites were relatively close to each other, the researchers assumed that other ecological variables that might affect group size (such as predators) were similar across sites and so had little effect on their results.

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**FIGURE 15.10. Primate group sizes.** The average group size in two species of primates correlated positively with the density of food-producing trees (trees/ha). Circles are red-tailed guenons; triangles are red colobus. Names denote populations. (Source: [Chapman & Chapman 2000](#))

## FEATURED RESEARCH Sociality and disease transmission in guppies

Another important cost of group living involves the transmission of infectious diseases. Many parasites and pathogens reduce fitness ([Daszak, Cunningham, & Hyatt 2000](#)) and are transmitted by close contact. Contact between individuals increases with degree of sociality; it is therefore not surprising that there is often a positive correlation between group size and the proportion of infected individuals in a group ([Rifkin, 2012](#)). After all, individuals will frequently be in close proximity when group size is large ([Brown & Brown 1986](#)).

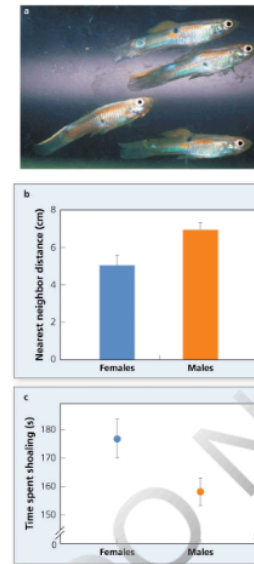
E. Loys Richards, Cock van Oosterhout, and Joanne Cable examined how the degree of sociality affects parasite transmission in guppies (*Poecilia reticulata*) ([Richards, van Oosterhout, & Cable 2010](#)). Guppies are small tropical fish that live in small shoals (or schools). They are frequently infected with external parasitic worms, such as *Gyrodactylus turnbulli*, that attach to their fins, gills, and scales. Female guppies tend to spend more time in schools than males, and the researchers took advantage of this variation in behavior to examine differences in disease spread in schools of either females or males.

The researchers first removed all external parasites from a population of guppies. They placed groups of six males or six females in separate tanks, choosing one randomly selected focal guppy in each tank and identifying it by its unique color markings. To quantify the degree of sociality, each group was observed every 30 seconds during a 15-minute period for three days. The research team noted the distance of the nearest neighbor from the focal fish and the maximum school size, defined as the number of guppies within four body lengths of one another. At the end of the third day, the focal fish was infected with approximately 100 *G. turnbulli* worms and then placed back with its school to potentially infect others. Three days later, all fish were inspected for parasite infection.

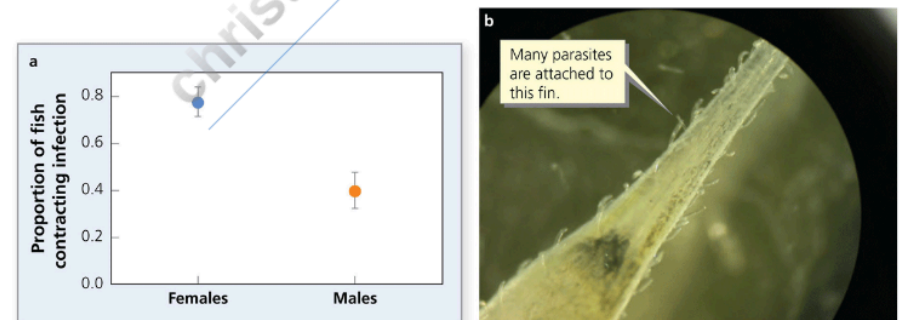
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with its school to potentially infect others. Three days later, all fish were inspected for parasite infection.

As expected, female groups spent more time schooling and had tighter groups than males—that is, females exhibited a higher degree of sociality ([Figure 15.11](#)). After the parasite was introduced, the researchers found that almost 80% of the females in each tank became infected, while only 40% of the males became infected ([Figure 15.12](#)). These results suggest that parasite transmission in guppies is affected by social behavior, with greater time spent near others, as in the female schools, leading to higher rates of transmission.



**FIGURE 15.11. Guppy shoaling.** (a) School of guppies. (b) Mean ( $\pm$  SE) nearest neighbor distance and (c) mean ( $\pm$  SE) time spent shoaling for males and females. Female guppies were more tightly spaced and spent more time shoaling than males. (Source: [Richards, van Oosterhout, & Cable 2010](#))



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**FIGURE 15.12. Infection rates.** (a) Females had higher mean ( $\pm$  SE) infection rates than males in the experiment. (b) *G. turnbulli* parasitic worms attached to the fin of a guppy. (Source: Richards, van Oosterhout, & Cable 2010)

We have examined several of the benefits and costs associated with life in groups. When the benefits of sociality are large relative to the costs, we expect to see individuals living in groups. When the benefits are low and the costs are high, we expect to see small group sizes or a lack of sociality. This understanding is being used to benefit social groups housed in captivity ([Applying the Concepts 15.2](#)).

### APPLYING THE CONCEPTS 15.2

#### Group size of social species in captivity

Group size in the wild is often strongly affected by antipredator benefits or competition for food. For captive animals, these factors are irrelevant, meaning that the group size typical in the wild may often not be best for animals in captivity. What, then, is the best group size for the latter?

Elizabeth Price and Tara Stoinski have shown that many social species suffer high levels of stress when forced to live in captivity with an inappropriate number of conspecifics ([Price & Stoinski 2007](#)). Social species that are housed with too few individuals often exhibit signs of chronic stress and reduced reproduction. For example, gorillas housed as breeding pairs have lower reproductive success than gorillas housed in groups of three or more ([Maple & Hoff 1982](#)). Stress, increased levels of aggression, and reduced reproductive success also occur when densities in captivity are too high. Duikers are an instructive example. The Los Angeles Zoo initially housed duikers in groups of five, but individuals often developed stress-related jaw abscesses and lived less than five years. When group size was reduced to no more than three, individual health and life span both increased dramatically ([Barnes et al. 2002](#)).

Price and Stoinski suggest that naturally observed group size in the wild may not be the best group size in captivity. To minimize stress and aggression from overcrowding, Price and Stoinski suggest that institutions create captive environments with greater structural complexity. For example, zoos can provide animals with both visual barriers and escape paths so that individuals can modify their proximity to others. ■

As we have seen, competitive interactions are an important cost of living with others, and they can be particularly intense in social groups. In the next section, we examine how the frequency of aggressive interactions, and their associated costs, can be reduced in groups.

## 15.2 Dominance hierarchies reduce the social costs of aggression

### Learning Objectives

After reading this section, you should be able to

- describe how a dominance hierarchy can benefit individuals in a group and
- compare the benefits of dominance hierarchy formation between dominants and subordinates in a group.

In many groups, individuals will vary in their competitive abilities based on age, size, or condition, and so some individuals will be better competitors than others. In general, more competitive individuals will have greater access to limited resources than will weaker rivals, resulting in greater net benefits of group membership ([Vehrencamp 1983](#)). Engaging in aggressive interactions over resources runs the risk of injury for both parties involved, a substantial cost of sociality. In most groups, repeated encounters between two individuals usually end in the same result: the better competitor wins the interaction. Given this predictability of outcomes, one way to minimize aggression within groups is through the formation of a **dominance hierarchy**, an organized social system with dominant and subordinate members. In a **linear dominance hierarchy**, an individual is dominant to each individual below it and subordinate to all above it in rank. The formation of such dominance hierarchies benefits group members in two ways: individuals have a chance to accrue the benefits of high status, and low-ranking individuals suffer reduced aggression from dominants. Let's look at studies of crayfish and baboons to see how dominance hierarchies benefit individuals in social groups.

### FEATURED RESEARCH Dominance hierarchies and crayfish

Crayfish are small freshwater crustaceans that feed on a wide variety of foods, including living and dead animals and plants ([Figure 15.13](#)). They are relatively sedentary and live and feed on stream bottoms. When aggregated in high densities, they often fight over resources and form dominance hierarchies. In such contests, they exhibit both aggressive and submissive behaviors. The former include approach, in which crayfish move toward an opponent; threat display, in which they spread their claws; and attack, in which they move quickly toward an opponent with claws open. The latter include retreat and escape. A retreating individual slowly moves away from an opponent, whereas an escaping individual moves rapidly.





FIGURE 15.13. Crayfish. Crayfish live and feed on stream bottoms.

#### Video: Crayfish in stream defending food

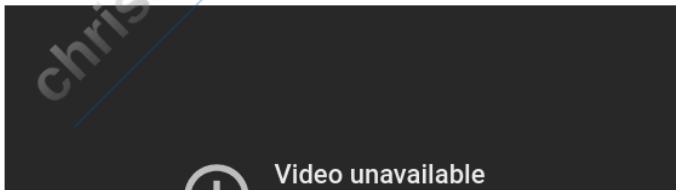
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Video: Crayfish in stream defending food



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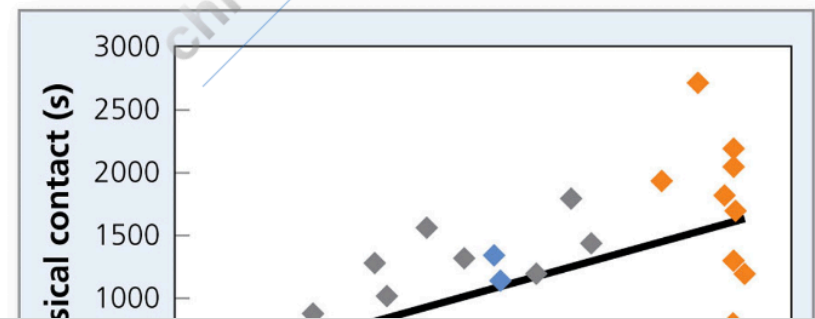
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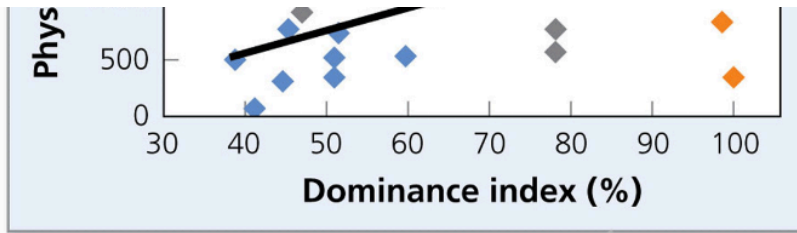
Jens Herberholz, Catherine McCurdy, and Donald Edwards studied the benefits of a social dominance hierarchy in juvenile crayfish (*Procambarus clarkii*) (Herberholz, McCurdy, & Edwards 2007). Because the species does not live in permanent social groups, the research team first investigated whether it forms dominance hierarchies in the absence of a resource. Second, they asked whether the formation of a hierarchy reduces aggression and determines access to food.

The team conducted a simple but elegant experiment. They placed three individuals, uniquely marked with dots of color on their carapace, into an aquarium (15 cm × 30 cm × 20 cm) that was divided into two compartments by an opaque partition. Individuals were placed in the larger compartment, and all agonistic interactions were recorded for 30 minutes in the absence of any resource. Next, a piece of chicken liver was placed in the other compartment, and the opaque partition was lifted. The researchers recorded the number of aggressive and submissive behaviors exhibited by each individual, both in the absence and in the presence of the food, to calculate a dominance index (defined as the number of aggressive acts divided by the total number of aggressive plus submissive acts). They also recorded the proximity of each individual to the food to determine the individual's access to it. This experiment was repeated for ten sets of three crayfish.

In each trio, crayfish displayed high levels of aggression. In the first part of the experiment and in the absence of a resource, aggression levels were high and a linear dominance hierarchy was established. The researchers identified a top-ranked alpha individual that possessed the highest dominance index, a second-ranked beta individual, and a third-ranked gamma individual that possessed the lowest dominance index. However, once the dominance hierarchy had been established, aggression levels decreased by 80% in the second part of the experiment, even though food was present. As expected, dominance rank strongly affected access to the food. Individuals with higher ranks spent more time in contact with the food than did lower-ranked individuals (Figure 15.14). The researchers concluded that dominant crayfish have greater access to resources than subordinate crayfish, and that the formation of a dominance hierarchy significantly reduces aggressive interactions among individuals. Once relative dominance ranks are formed, there is little to gain from continued aggression, reducing the cost of living in social groups. Next, we examine how dominance hierarchies can reduce stress in social groups of baboons.



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**FIGURE 15.14. Dominance status.** The most dominant alpha males (orange) tended to spend the most time in contact with food. Beta individuals (gray) spent more time in contact with food than the lowest-ranking gamma individuals (blue). (Source: [Herberholz, McCurdy, & Edwards 2007](#))

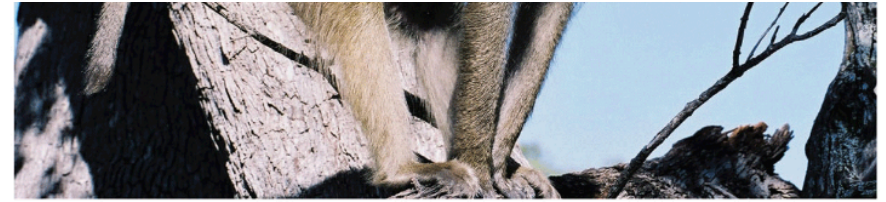
## FEATURED RESEARCH Stable dominance hierarchies in baboons

Aggressive interactions are a source of stress, and **glucocorticoids** are hormones that are secreted by the adrenal gland in vertebrates in response to stressful situations. Chronic stress is associated with altered immune system function and reduced reproduction and thus negatively impacts fitness ([Sapolsky 2005](#)). If dominance hierarchies function to reduce aggression within groups, they should also lessen stress. Conversely, any disruption in the dominance hierarchy could result in increased stress levels.

Thore Bergman and his colleagues investigated whether an unstable dominance hierarchy could result in increased stress in chacma baboons (*Papio hamadryas ursinus*) ([Figure 15.15](#)) ([Bergman et al. 2005](#)). For over 14 months, the team studied a population in the Moremi Game Reserve in Botswana. This population had been intensively studied for decades (e.g., [Bulger & Hamilton 1987](#)), and so the researchers knew that its males form a strict linear dominance hierarchy in which alpha males have sole access to fertile females. However, this population also lives near other groups (which allows males to easily move between groups); shifts in rank are common, with the identity of the alpha male changing, on average, about every six months.



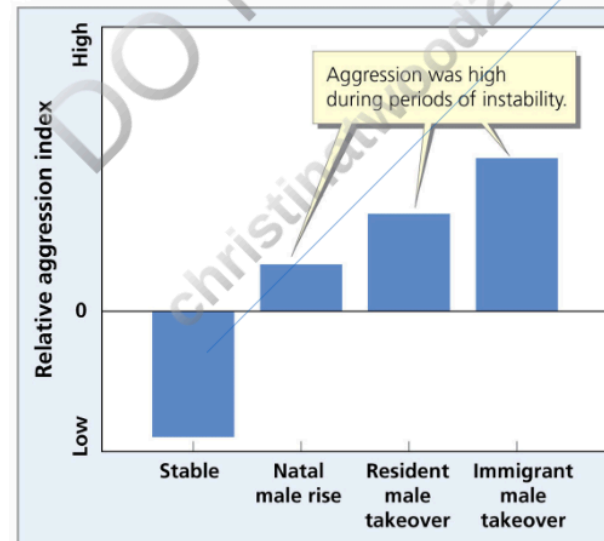
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**FIGURE 15.15. Chacma baboons.** These Old World primates are found throughout southern Africa.

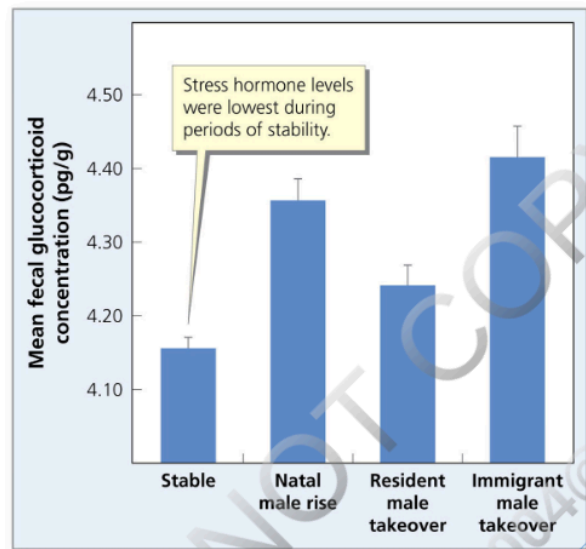
The research team conducted over 1,000 ten-minute scans to record male aggression and collected 482 fecal samples to measure glucocorticoid levels (using a radioimmunoassay procedure) ([Beehner & Whitten 2004](#)). Each sample was time coded, and at least seven samples were collected for each male. The researchers divided the study into periods in which the dominance hierarchy was either stable (times with no change in alpha or beta males) or unstable (times during which the alpha or beta male changed). During the study, there were five periods of instability interspersed with two stable hierarchy periods of two to three months each.

Instability strongly increased aggression among males, whereas aggression remained below average during stable periods ([Figure 15.16](#)). Male fecal glucocorticoid levels varied with dominance stability, just as predicted. Stress hormone levels were lowest during stable periods but were significantly higher during each period of instability ([Figure 15.17](#)). The increase in glucocorticoid levels during periods of instability occurred in both high- and low-ranking males. Therefore, the stable dominance hierarchy has important fitness consequences for all males in the group by reducing potential costs of high levels of aggression in social groups.



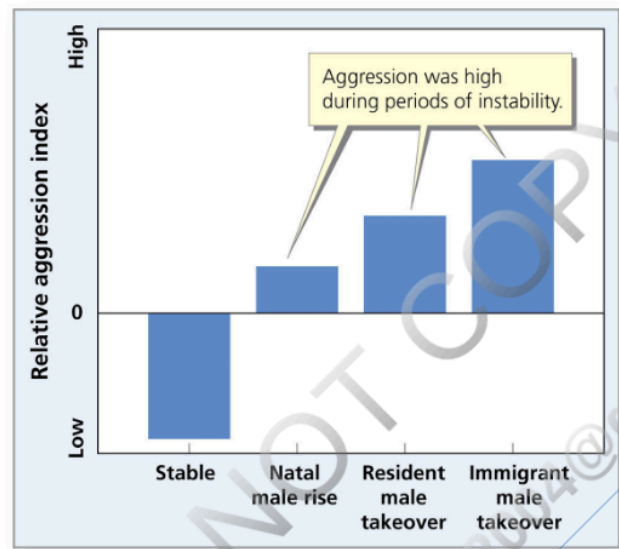
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**FIGURE 15.16. Male aggression levels.** Male aggression was low when the dominance hierarchy was stable. Aggression levels were higher during periods of instability in the group dominance hierarchy. (Source: [Bergman et al. 2005](#))

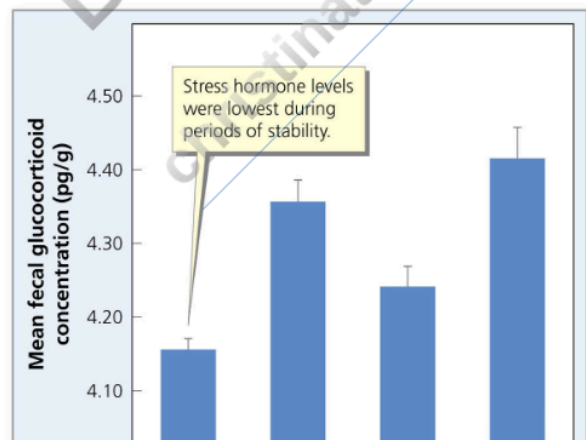


**FIGURE 15.17. Stress hormone levels.** Mean (+ SE) male fecal glucocorticoid levels were lowest (indicating low stress) during stable periods. (Source: [Bergman et al. 2005](#))

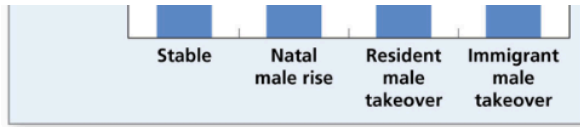
during each period of instability ([Figure 15.17](#)). The increase in glucocorticoid levels during periods of instability occurred in both high- and low-ranking males. Therefore, the stable dominance hierarchy has important fitness consequences for all males in the group by reducing potential costs of high levels of aggression in social groups.



**FIGURE 15.16. Male aggression levels.** Male aggression was low when the dominance hierarchy was stable. Aggression levels were higher during periods of instability in the group dominance hierarchy. (Source: [Bergman et al. 2005](#))







**FIGURE 15.17. Stress hormone levels.** Mean (+ SE) male fecal glucocorticoid levels were lowest (indicating low stress) during stable periods. (Source: [Bergman et al. 2005](#))

### 15.3 Ecology and phylogeny influence the evolution of sociality

#### Learning Objectives

After reading this section, you should be able to

- describe habitat–sociality associations and
- explain how the comparative method is used to understand the variation in sociality among species.

We have seen that many factors influence the advantages and disadvantages of living with others. Examination of [Table 15.1](#) suggests that ecological conditions may strongly influence many fitness benefits and costs. For instance, species living in open habitats with few safe refuges from predators might derive greater antipredator benefits from social living than those living in dense vegetation with many refuges. Indeed, studies of both primates and toothed whales show such an association: social species are most often found in open habitats, while solitary and pair-living species are mostly found in dense or closed habitat ([Janson & Goldsmith 1995](#); [Gygax 2002](#)).

Variation in sociality among a closely related group of species may result from the influence of ecology (habitat conditions) on fitness benefits and costs, but species differences in group living may also represent a historical legacy of ancestor–descendent relationships: evolution of sociality can be constrained by phylogeny, and so a species might be asocial because it evolved from an ancestor that was not social. Understanding how ecological conditions and phylogeny influence the evolution of sociality in a group of species often involves the comparative method. Let's examine two such studies that show how environmental conditions and phylogeny influence the evolution of social living in rodents and ungulates.

#### FEATURED RESEARCH Evolution of rodent sociality and habitat use

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The hystriognath rodents are a large group that includes well-known species such as domestic guinea pigs (*Cavia porcellus*) and capybaras (*Hydrochoerus hydrochaeris*) ([Figure 15.18](#)). They exhibit a wide range of sociality, from solitary porcupines to mole rats that live in large colonies across a variety of environments, including open grasslands, as well as closed shrubland and forest habitats.



**FIGURE 15.18. Capybara.** A large hystriognath rodent.

Raúl Sobrero and his colleagues examined the evolution of social behavior in this group by constructing a phylogeny of 98 species from both the New and Old World using DNA sequence data from GenBank ([Sobrero et al. 2014](#)). For each species, they classified whether it was social or solitary and its habitat use as open, closed, or mixed (i.e., riparian, swampy, or mangrove) based on the main habitat type it was found in. Finally, they categorized each species as subterranean or not based on whether they conduct most of their living below or above ground. The resulting data were used in their comparative analysis to reconstruct the evolutionary relationships and habitat use in the group.

The analysis indicated that the common ancestor of the group was most likely a social species that lived in open habitats. Subsequently, we see the evolution of solitary species, often in conjunction with the use of closed habitats. Vegetation cover was associated with group living: social species were found in habitats with lower values of vegetation cover. However, group living was not predicted by whether a species was subterranean. This comparative approach not only provides insight into the variation in sociality and habitat use in this group but also shows how often sociality and the use of different habitats evolved.

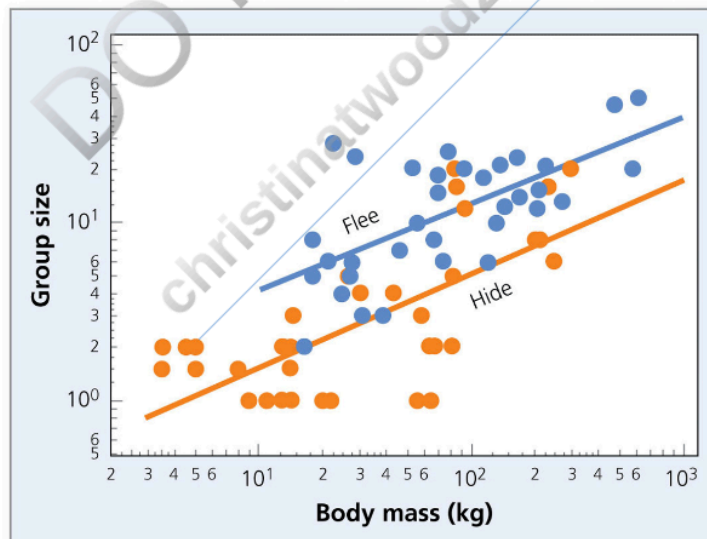
#### FEATURED RESEARCH Body size, diet, and habitat

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## FEATURED RESEARCH Body size, diet, and habitat influence sociality in antelope

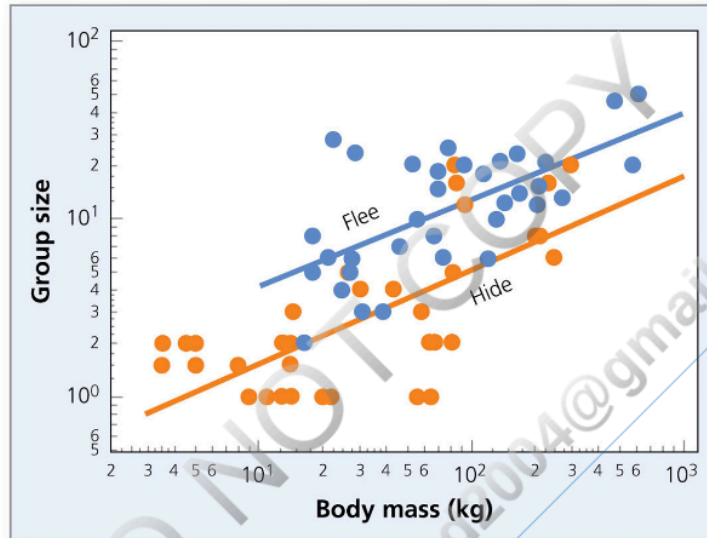
Such habitat–sociality associations are not restricted to rodents. In a classic study, Peter Jarman described the ecology and behavior of several dozen African antelope species (Jarman 1974). He found a wide range of ecological and behavioral traits among the species: diets ranged from browse specialists to grass generalists; species that lived in open grassland tended to flee from predator attack, while others living in dense woody vegetation tended to hide from predators; and social associations ranged from solitary or paired individuals to those that lived in large groups. In addition, body mass ranged from 4 kg to over 500 kg. Jarman suggested that the degree of sociality correlated with body size, habitat use, diet, and antipredator behavior as follows: small species tended to live in small social groups and in dense vegetation, hide from predators rather than flee, and were dietary specialists, while large species tended to live in large groups in open habitats and flee from predator attacks, and were dietary generalists.

While Jarman's study has been influential, his conclusions were based on correlations and did not account for phylogenetic relatedness among species. Justin Brashares, Theodore Garland, and Peter Arcese reexamined the traits of these same species using statistical techniques that account for the nonindependence of species due to evolutionary relatedness (Brashares, Garland & Arcese 2000). Their analyses supported Jarman's conclusions: large species that live in open habitat and feed on a wide array of grasses are highly social, while smaller species live in dense forest habitat, browse selectively on woody vegetation, tend to live in much smaller social groups, and hide from predators rather than flee (Figure 15.19) (Brashares, Garland, & Arcese 2000). Each of these studies shows how examination of ecological conditions and evolutionary history can help to explain variation in sociality among closely related species.



**FIGURE 15.19.** Morphological, ecological, and behavioral traits in African ungulates. Each point represents a species. Species that flee when attacked are blue and species that hide when attacked are orange. Larger species tend to live in groups of larger size and flee when attacked. (Source: Brashares et al. 2000)

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## 15.4 Hormones regulate social behavior

### Learning Objectives

After reading this section, you should be able to

- describe how hormones can regulate social behavior and
- design a research study to examine the effect of hormones on social behavior.

Across species we see much variation in degree and maintenance of social relationships, known as affiliative behavior. Such variation can also be seen within individuals over time. For instance, individuals may be highly social in the nonbreeding season but then defend territories by themselves or in pairs in the reproductive season. How is such variation in behavior regulated?

Like all behaviors, the tendency to affiliate with others results from a combination of genetic, developmental, and environmental factors mediated by neural and molecular mechanisms. One particular focus has been on the mammalian neurohormones oxytocin (OXT) and arginine vasopressin (AVP), as well as their homologues in other taxa. These neuropeptides are produced in the hypothalamus and can be released centrally to other neurons in the brain and peripherally into the bloodstream. Much work on these neuropeptides has focused on the simplest forms of affiliative behavior, such as showing a social preference for a partner or offspring, or investigative and grooming behavior of unfamiliar conspecifics in laboratory animals. For instance, Cort Pedersen, John Ascher, Yvonne Monroe, and Arthur Prangle Jr. studied maternal behavior in female mice, such as licking, crouching over, and retrieval of pups (Pederson et al. 1982). Virgin mice have low OXT levels and do not exhibit these behaviors; in contrast, almost immediately after parturition, adult female OXT levels rise and mothers rapidly exhibit such maternal affiliative behaviors.

To experimentally demonstrate that maternal behavior is influenced by oxytocin, Pedersen and his colleagues used virgin, ovariectomized females. The mice's brains were infused with either a particular dose of OXT or a saline control. Individuals were placed in an observation cage with three unrelated pups and nesting material and were observed for three hours. Maternal behavior correlated positively with the dose of OXT administered (Pedersen et al. 1982).

In a similar manner, Larry Young and his colleagues studied how AVP influenced affiliative behavior in prairie voles (*Microtus ochrogaster*) (Young et al. 1999). Vole species differ greatly in their social behavior and mating system. Prairie voles are highly affiliative, monogamous, and exhibit biparental care for the offspring, while most other species are relatively asocial and promiscuous, and only females care for the offspring. Young and his colleagues experimentally manipulated AVP in male prairie voles. They placed test males in one side of a two-chambered arena with an ovariectomized female on the other side. Half the males were treated with 2 ng of AVP delivered to the brain while control males were infused with artificial cerebrospinal fluid. Treatment males exhibited significantly more affiliative behavior toward the female (olfactory inspection and grooming) compared to control males.

These and many other studies have shown that both oxytocin and arginine vasopressin modulate social behavior in laboratory conditions. Additional investigations have examined a greater diversity of species, other aspects of sociality, and free-living species. Let's look at three such studies.

### FEATURED RESEARCH Social approach behavior and neuropeptides in goldfish

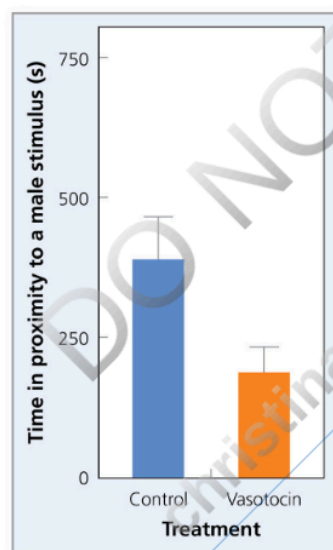
Goldfish (*Carassius auratus*) frequently live in loose shoals. Isolation is stressful (Laudien et al. 1986), and solitary individuals will typically move toward conspecifics in a nonaggressive, investigative manner, a form of affiliative behavior. Richard Thompson and James Walton tested the hypothesis that centrally administered vasotocin (VT) and isotocin (IT)—the homologues of mammalian oxytocin and arginine vasopressin in fish—



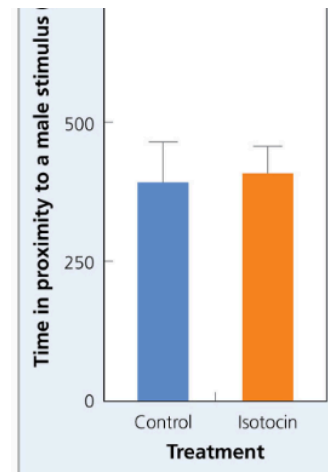
would inhibit and promote, respectively, such social investigation by individuals (Thompson & Walton 2004).

The research team implanted a small cannula to centrally infuse saline or a drug into the ventricle of the brain of male goldfish. After three days of recovery, test fish were placed into a central compartment flanked by two side compartments, or stimulus chambers; the areas were separated by Plexiglas to prevent water flow and olfactory communication. In the first experiment, each test fish was infused over two days with saline (control) or 1 microliter ( $\mu\text{L}$ ) of 200 ng/ $\mu\text{L}$  of VT. In a second experiment using different individuals, each test fish was infused a saline control or 200 ng/ $\mu\text{L}$  of IT. Five minutes after injection, a stimulus male conspecific was placed in one of the stimulus chambers, and the research team recorded the time the test fish spent with its nose within 1 cm of the partition, a measure of affiliative behavior by the test fish.

The VT treatment resulted in lower levels of affiliative behavior (Figure 15.20). However, there was no effect of the IT treatment on time spent near a conspecific (Figure 15.21). The researchers did note that there was much variation in affiliative behavior among individuals in response to both VT and IT treatments, and so more work needs to be done to understand this variation. Overall, these results do suggest that variation in goldfish sociality can be influenced by the actions of neuropeptides.



**FIGURE 15.20. Vasotocin inhibits affiliative behavior in fish.** Mean (+ SE) time in proximity to a stimulus fish for controls (saline injected—blue bar) and treatment (vasotocin injected—orange bar). (Source: Thompson & Walton 2004)



**FIGURE 15.21. Isotocin and affiliative behavior in fish.** Mean (+ SE) time in proximity to a stimulus fish for controls (saline injected—blue bar) and treatment (isotocin injected—orange bar). (Source: Thompson & Walton 2004)

## FEATURED RESEARCH Mesotocin and pro-social behavior in finches

Many studies, like the previous one on goldfish, allow focal subjects the choice of being social or not. Ultimately, we'd also like to determine how hormones affect behavior when individuals are given more subtle options, such as joining a small or large group of individuals. These choices are common for many species, including social birds.

Zebra finches (*Taeniopygia guttata*) are a monogamous species native to Australia that lives in large flocks of up to 300 individuals. James Goodson and his colleagues tested the prediction that experimental addition of mesotocin

## CHAPTER SUMMARY AND BEYOND

Living in groups can benefit individuals through enhanced foraging success, reduced costs of movement, greater safety from predators, and the potential for individual specialization. However, it also comes with important costs, such as increased competition for resources, increased aggressive interactions, and enhanced disease transmission. Variation in costs and benefits helps explain observed variation in sociality and group size ([Curley et al. 2015](#); [Markham et al. 2015](#)).

Many social groups are structured by dominance hierarchies, which can reduce one cost of living with others. While dominant individuals gain greater access to resources, subordinates suffer less aggression once the hierarchy is established. Stable dominance hierarchies also reduce stress. However, Gesquiere and colleagues found that the most dominant individual can experience the highest level of stress within a stable hierarchy, so more work on this subject is needed ([Gesquiere et al. 2011](#)).

Ecological conditions, such as habitat structure, can also influence the evolution of sociality. Open habitats with high predation risk tend to favor larger group sizes compared to more closed habitats. Comparative studies reveal how body size, along with ecological conditions, influence the evolution of sociality in related species. [Thierry, Iwaniuk, and Pellis \(2000\)](#) provide an additional example in primates. Hormones such as oxytocin, arginine vasopressin, and their homologues modulate social behavior as well; experimental manipulation of these hormones alters the tendency of individuals to associate with others. Reviews of work on a variety of species documenting relationships between these hormones and social behavior can be found in [Stoesz, Hare, and Snow \(2013\)](#); [Caldwell \(2017\)](#); and [Smith et al. \(2017\)](#).

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## CHAPTER 14

# Parental Care

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
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### Concepts

- 14.1 [Parental care varies among species and reflects life history trade-offs](#)
- 14.2 [Sexual conflict is the basis for sex-biased parental care](#)
- 14.3 [Parental care involves fitness trade-offs between current and future reproduction](#)
- 14.4 [Brood parasitism reduces the cost of parental care and can result in a coevolutionary arms race](#)
- 14.5 [Hormones regulate parental care](#)

### Features

#### Scientific Process

- 14.1 [Paternity certainty and parental care in bluegill sunfish](#)
- 14.2 [Parental care costs in eiders](#)
- 14.3 [Brood reduction in blackbirds](#)

#### Applying the Concepts

- 14.1 [Human life history trade-off](#)
- 14.2 [Smallmouth bass defend their nest from exotic predators](#)
- 14.3 [Food supplementation reduces brood reduction in endangered eagles](#)

#### Quantitative Reasoning

- 14.1 [Prey provisioning rates of American kestrels](#)

Each spring we enjoy watching animals care for their young. We have observed both male and female eastern phoebes (*Sayornis phoebe*) feeding their chicks in a nest under our deck and a Virginia opossum (*Didelphis virginiana*) carrying young on her back. Although phoebe offspring receive care from both parents, the opossum young receive care from only one parent, their mother. In many fish, too, care is often provided by just one parent

young receive care from only one parent, their mother. In many fish, too, care is often provided by just one parent—but which sex provides care varies across species (Figure 14.1). We've often seen male fish defending their nest during our snorkeling trips. And, while many birds, mammals, and fish provide care for their young, care is minimal in many other taxa. For example, female spotted salamanders (*Ambystoma maculatum*) lay egg masses in a stream near our house but then depart and provide no direct care for their growing young.

In this chapter, we first examine variation in parental care across taxa and discuss why one sex typically provides more care than the other. We then see how researchers explain variation in parental care among individuals within a species and over their individual lifetimes. Next, we examine brood parasitism, a reproductive strategy that reduces the costs of parental care. Finally, we examine how parental care behaviors are regulated.



FIGURE 14.1. Parental care. An anemonefish guards eggs in a nest.

### Video: Male clownfish caring for eggs from spawning until hatching

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Video: Male clownfish caring for eggs from spawning until hatching

These are common ways for eggs from spawning and nesting

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## 14.1 Parental care varies among species and reflects life history trade-offs

### Learning Objectives

After reading this section, you should be able to

- provide examples of life history traits and
- utilize life history theory to predict trade-offs between life-history traits.

**Parental care**, the activities of an adult that enhance the survivorship of offspring, includes nourishing and incubating eggs and young, defending them from predators, and sometimes transporting them. If parental care increases offspring survival, why don't all species provide high levels of care to their young? The answer is found in life history theory.

Animals vary greatly in their **life history traits**—traits involved with growth, reproduction, and survivorship that are the result of natural selection. These traits include age at first reproduction, number and size of offspring, level of parental care, and survival rate throughout life. For example, elephants do not become sexually mature until 13 years of age; reproduce only about every five years; have a gestation period of 22 months; give birth to a single, very large calf; and provide parental care for several years. Each calf has a fairly high likelihood of surviving because of the enormous amount of parental care it receives and its large size, which decreases the risk of predation. By contrast, fruit flies mature in a few weeks, and females can produce hundreds of eggs over their brief life span, but parents provide no direct care to their offspring, each of which has a low survivorship. Even more extreme cases are some marine fish, such as cod, that become sexually mature within a few years and can produce 4 to 6 million small eggs at a single spawning. Again, these eggs receive minimal parental care, and only a few may survive to reproduce.

**Life history theory** proposes that natural selection will favor the evolution of traits that maximize an individual's lifetime reproductive success. For all animals, energy (or effort) is allocated not only to one's self for growth and maintenance but also to offspring in the form of reproduction and parental care. The limited available energy creates an important life history trade-off: effort allocated toward reproduction and parental care reduces the effort that can be allocated toward an individual's own growth and survival ([Applying the Concepts 14.1](#)).

### APPLYING THE CONCEPTS 14.1

#### Human life history trade-off

Reproduction and parental care involve high energetic investment for many female animals, particularly mammals. Such costs are part of a common life history trade-off between



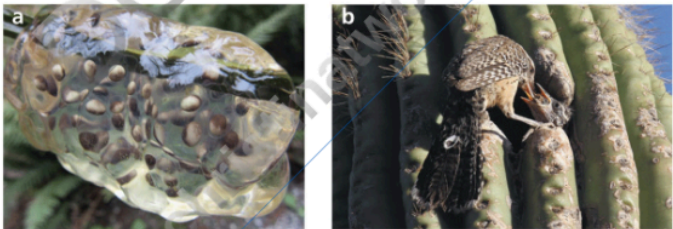
particularly mammals. Such costs are part of a common life history trade-off between reproduction and survivorship. Do human females experience a life history trade-off between reproduction and longevity?

Rudi Westendorp and Thomas Kirkwood investigated this question using genealogical records from over 2,000 women who were members of the British aristocracy between the years 740 and 1876 (Westendorp & Kirkwood 1998). Detailed records for each woman indicate her age at first childbirth, number of progeny, and age at death.

Among women who lived at least 60 years (and presumably had reached menopause), there was a significant negative correlation between number of progeny and life span. In addition, there was a significant positive correlation between longevity and age at which a woman first gave birth.

These data reveal that women of the British aristocracy who had long life spans tended to have fewer offspring and to have begun reproduction at a later age than women who had shorter life spans. This pattern is concordant with a life history trade-off between reproduction and survivorship. ■

This trade-off allows us to understand the evolution of life history traits across species, including parental care behavior (Clutton-Brock 1991). Across species, we often see the evolution of particular sets of life history traits along a continuum. At one end, natural selection can favor individuals that produce many small offspring and provide minimal parental care, while at the other end, selection can favor the evolution of individuals that produce fewer but larger offspring that receive much parental care (Figure 14.2). In general, taxa that have a longer life span produce a relatively small number of large offspring and exhibit higher levels of parental care compared to those with a short life span, which tend to produce many small offspring (e.g., Strathman & Strathman 1982; Kolm & Ahnesjö 2005; Summers, Sea, & Heying 2006). Let's examine evidence of these life history patterns in fish.



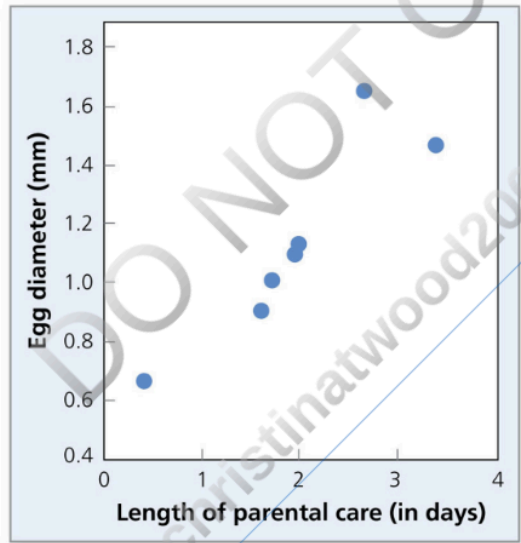
Life history trait	Species A	Species B	Species C
Fecundity	High	Intermediate	Low
Survivorship	Low	Intermediate	High

Parental care	Low	Intermediate	High
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**FIGURE 14.2. Life history continuum.** (a) Salamander eggs. (b) Cactus wren (*Campylorhynchus brunneicapillus*) feeding young. (c) High levels of parental care are typically seen in species that produce few large offspring—those with low fecundity and high survivorship, such as Species C. Species A exhibits low levels of care and has high fecundity and low survivorship. Species B exhibits intermediate life history trait values.

## FEATURED RESEARCH Life history variation in fish

Fish display tremendous variation in life history and illustrate how parental care varies across species. For example, in the sunfish family, species vary in the duration of parental care provided to offspring, ranging from one day to a few weeks (Gross & Sargent 1985). And, as one might expect from life history theory, species that provide more care are those that produce fewer and larger eggs (Figure 14.3).



**FIGURE 14.3. Parental care and egg diameter.** Across species of sunfish, the duration of parental care and egg size co-vary positively. Each point represents one species. (Source: Sargent, Taylor, & Gross 1987)

Anna Vila-Gispert and her colleagues conducted a comparative study to examine additional variation in life history trait patterns among more than 300 fish species from Europe, North America, and South America (Vila-Gispert, Moreno-Amich, & García-Berthou 2002). For each species, the researchers used published work as well as their own data to estimate life history traits such as age at maturity, maximum body size (standard length), length of breeding season, number of reproductive events per year, average egg size, fecundity (average number

of oocytes in a single mature ovary), and level of parental care (amount of protection and nourishment of offspring).

The researchers found that although there was much variation in life history traits among species, species with larger body size tended to have higher fecundity, later maturation, and fewer reproductive events per year. Species with smaller body size showed the opposite trends. Additionally, species with more parental care also tended to have larger eggs. These patterns reflect the basic life history trade-off: species that invest more in individual offspring (indicated by large egg size) tend to also provide greater levels of parental care. The researchers also found that these patterns held up over different geographic areas and habitats, as well as across different fish taxa.

The great variation in life history traits across taxa helps explain much variation in care provided across species. This care ranges from minimal, to care provided only by females (maternal care), care provided only by males (paternal care), or care provided by both sexes (biparental care) (Reynolds, Goodwin, & Freckleton 2002). In vertebrates, certain major trends of parental care are evident across taxa: most amphibians and reptiles provide little parental care, birds provide predominantly biparental care, and mammals often provide extensive and mainly maternal care (Table 14.1). While less common than in vertebrates, parental care has evolved in many invertebrates, including at least 12 orders and 50 families of insects, and 16 lineages of arthropods (Trumbo 2012).

**TABLE 14.1 Parental care in selected vertebrate groups.** Numbers are the percent of species that exhibit a particular type of care.

Taxon	Type of Parental Care (Percent of Taxon)			
	Minimal Care	Female Only	Male Only	Biparental
Fishes (422 families)	80	6	10	4
Cichlid fish (Cichlidae; 182 genera)	0	60	<1	40
Frogs and toads (Anurans; 315 genera)	91	4	4	1
Lizards and snakes (938 genera)	97	3	0	0
Crocodiles and alligators (21 species)	0	62	0	38
Birds (9,450 species)	0	8	1	91
Nonprimate mammals (1,117 genera)	0	91	0	9
Primates (203 species)	0	68	0	32

(Source: Reynolds, Goodwin, & Freckleton 2002; Cockburn 2006)

Males and females may both care for offspring in many species, but rarely do both sexes provide the same level of care. We examine that pattern next.

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## 14.2 Sexual conflict is the basis for sex-biased parental care

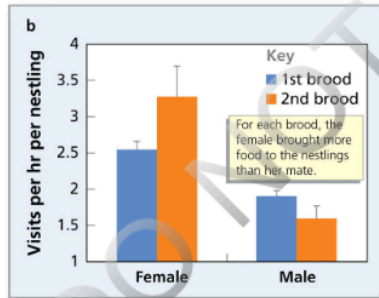
### Learning Objectives

After reading this section, you should be able to

- compare the conditions required for female-biased and male-biased parental care to evolve and
- predict how the level of paternity certainty affects male parental care.

In species that provide parental care, we see an interesting pattern: one sex typically provides most or all of the

In species that provide parental care, we see an interesting pattern: one sex typically provides most or all of the parental care. Often, females provide more care than males. Even in birds that typically exhibit biparental care, the female typically provides greater care than her mate. For example, Kirk Stodola and colleagues examined parental care behavior in black-throated blue warblers (*Dendroica caerulescens*). These small songbirds often produce two clutches each summer and exhibit biparental care. Stodola's research team quantified the rate at which males and females brought food to their nestlings. For both broods raised, females consistently brought more food than their mates to offspring (Figure 14.4) (Stodola et al. 2009). Why is parental care so often female biased?



**FIGURE 14.4. Female parental care.** (a) Female black-throated blue warbler feeding young. (b) Mean (+ SE) visits to the nest. Female black-throated blue warblers provide more parental care than males in terms of food delivery for their first and second broods. (Source: Stodola et al. 2009)

## Female-biased parental care

To explain the unequal division of parental care, we must examine the fitness benefits and costs of providing parental care for each sex. Both sexes obtain the same fitness benefit from providing parental care: increased offspring survival. However, as we have seen, such care takes time and energy, and it may increase predation risk for the caring adult. These costs create a conflict of interest between the sexes: each sex will benefit if the other pays the cost of care. The difference between the sexes in their fitness interests is known as sexual conflict (Trivers 1972; Chapman et al. 2003).

How is this conflict resolved? The sex with the higher cost of care should provide less care, because its net benefit of care will be smaller (Queller 1997). In most species, females have a greater certainty than males about the identity of their offspring, because they lay eggs or give birth. Therefore, the benefit of parental care to females is

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rather straightforward. What about the benefit for males? Because females can mate with multiple males while fertile, males will always be less certain of whether they sired the offspring of any female they have inseminated. This reduced certainty is an important cost to males, because it results in the possibility that a male will end up providing care to another male's offspring—a very high cost of providing parental care. Thus, natural selection can favor males that reduce their level of parental care. In fact, we can predict that the less certain the paternity, the less care will be provided by males (Trivers 1972; Queller 1997). Let's look at a test of this prediction in birds.

## FEATURED RESEARCH Paternity uncertainty and parental care in boobies

The blue-footed booby (*Sula nebouxii*) is a large, colonially nesting seabird (Figure 14.5). In this species, a single male and female form a pair bond and raise offspring together. Parental care is extensive and shared, as they take turns incubating eggs for 40 days and then feed the developing chicks for another 140 days. If a male is uncertain of his paternity, will he provide as much care? Marcela Osorio-Beristain and Hugh Drummond conducted a removal experiment to answer this question (Osorio-Beristain & Drummond 2001).



**FIGURE 14.5. Blue-footed booby.** A female sits on her clutch of eggs.

While fertile, a female copulates frequently with her mate, beginning just before and continuing during egg laying. When her mate is absent, however, she may also copulate with other males. The researchers manipulated certainty of parentage for males by removing pair-bonded males for 11 hours during the fertile period of the females, which occurs a few days before egg laying. Control males were removed for the same period of time, but

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females, which occurs a few days before egg laying. Control males were removed for the same period of time, but only when female fertility was low, about 15 days before egg laying. Female fertility was assessed by visual inspection of the cloaca (the urogenital opening). When the cloaca is open and reddish, females are fertile; when it is closed and not reddish, females are not fertile. After the removal period, all males quickly returned to their mate.

Experimental and control males differed in their behavior once eggs were laid. Seven of the 16 experimental males removed the first egg laid by their mate from the nest. (The egg was later destroyed by predators.) No other eggs were removed. None of the 17 control males removed any eggs laid by their mate. The researchers concluded that for experimental males, certainty of paternity was low for the first egg laid, as the male had been away during his mate's fertile period and the female may have mated with another male. Because the pair copulates

offspring. In this system, males have high levels of paternity assurance because they frequently copulate with the female whose eggs they accept and then care for. This assurance helps explain the evolution of male-only care. Up to now, we have seen how differential costs of care between the sexes are linked to sex-biased care among species. We have also examined one life history trade-off involving the certainty of paternity that helps explain variation in care among individuals and species. Next, we examine another life history trade-off that helps to explain additional variation in parental care among individuals within a species.

**Video: Giant water bug eggs hatching**

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## 14.3 Parental care involves fitness trade-offs between current and future reproduction

### Learning Objectives

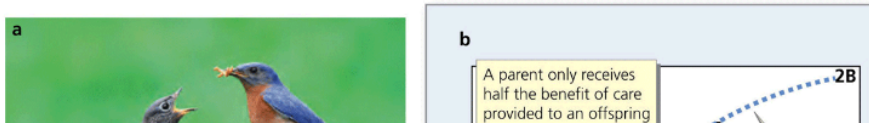
After reading this section, you should be able to

- use parent-offspring conflict theory to explain variation in parental investment,
- explain the fitness trade-off between current and future offspring, and
- describe how brood reduction can enhance fitness of parents.

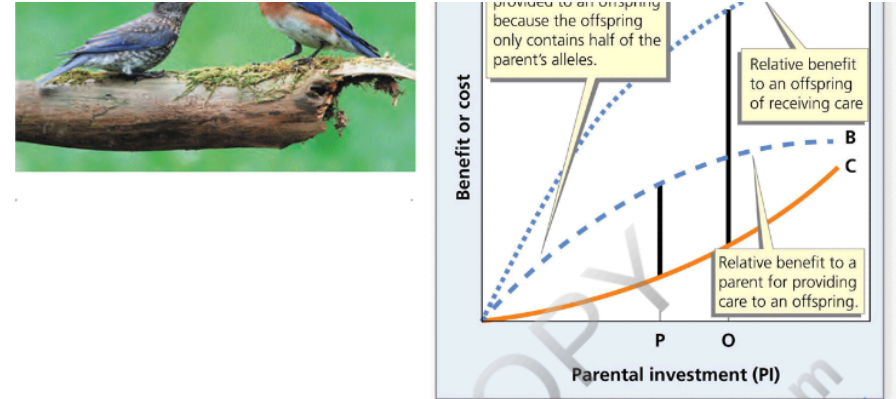
We have seen that sexual conflict offers an explanation for sex-biased parental care that is based on an important cost to males: paternity uncertainty. Another important fitness cost of parental care affects both males and females and involves a second life history trade-off: effort allocated toward current offspring reduces the effort that can be allocated toward future offspring. This trade-off also explains variation in the level of parental care exhibited by individuals in a population, and by parents to different siblings, as we see next.

### Parent-offspring conflict theory

The trade-off that adults face between current and future reproduction was first articulated by Robert Trivers. His **parent-offspring conflict theory** (Trivers 1974) states that parents and their dependent offspring are under different selection pressures: parents should maximize their lifetime reproductive fitness, while offspring should maximize their own fitness by obtaining as much energy and protection as they can from their parents to survive to reproductive age. Recall that Trivers described **parental investment** as costly investments by parents that increase the offspring's chance of survival (Trivers 1974). The benefit of parental investment is increased fitness of the offspring. However, the parent and the offspring obtain different benefits from parental investment, because the parent is related to the offspring by 0.5, whereas the offspring is related to itself by 1.0. The offspring therefore receives twice the fitness benefit from the care provided (Lazarus & Inglis 1986). In terms of reduced future offspring, however, the cost of parental investment is the same for both parent and offspring, since both are related to all future offspring by 0.5 (assuming full sibship) (Figure 14.7). Because the optimal level of parental investment is always higher for the offspring than for the parent, there is a parent-offspring conflict: the fitness of a parent is maximized at a lower level of investment than the fitness of an offspring.



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**FIGURE 14.7. Parent-offspring conflict theory.** (a) Eastern bluebird (*Sialia sialis*) chick begging for food. (b) The fitness benefit for offspring, 2B (blue dotted line), of receiving parental care is twice the fitness benefit for an adult, B (blue dash line), of providing care, because the coefficient of relatedness between parents and offspring is 0.5. The cost of parental investment, C (orange solid line), is in terms of reduced future offspring. Note that the optimal level of parental investment is higher for the offspring (O) than it is for the parent (P). (Source: Trivers 1974)

One basic prediction of parent-offspring conflict theory is that if the costs of parental care increase for a parent, the level of care provided to current offspring should decline. In the next section, we examine one test of this prediction in songbirds.

### FEATURED RESEARCH Predation risk and parental care in songbirds

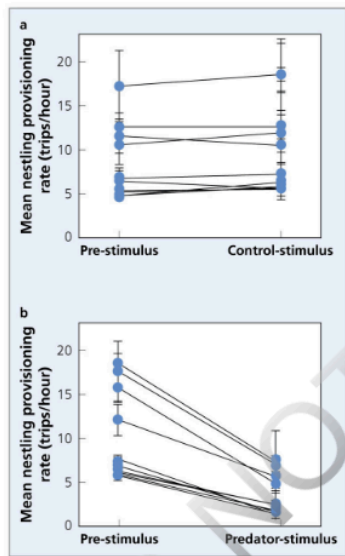
One common cost of parental care is predation risk. Adults that provide care are often more obvious to predators and so suffer higher mortality. Parent-offspring conflict theory predicts that parents should value their own survival over that of their offspring when predation risk is high. Cameron Ghalambor, Susana Peluc, and Thomas Martin tested this prediction by conducting an interesting comparative study in which they observed songbirds feeding their young and experimentally increased perceived predation risk (Ghalambor, Peluc, & Martin 2013).

The research team observed birds from ten species at sites in two locations (Arizona and Argentina) when adults were delivering food to their nestlings. The experimental design consisted of a 90-minute pre-stimulus control (no disturbance) followed by a 90-minute presentation of either a predator stimulus vocalization or a control stimulus vocalization. Vocalizations of Stellar's jays (*Cyanocitta stelleri*) (in Arizona) or plush-capped jays (*Cyanocorax chrysops*) (in Argentina) were used because they are common nest predators of songbirds in each location. The control stimulus was the vocalization of a tanager (*Piranga ludoviciana* or *Thraupis sayaca*), a common nonthreatening species. During each stimulus period, the research team recorded the number of nestling provisioning trips by the adults at each nest.

In each species, adults reduced the rate at which food was delivered to the nestling during the predator-stimulus

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treatment compared to the pre-stimulus period. In contrast, adult food delivery rates did not differ between pre-stimulus and control periods (Figure 14.8). This experiment illustrates that adults modify their level of parental care in response to a heightened risk of mortality and supports one key prediction of parent-offspring conflict theory.



**FIGURE 14.8. Nestling provisioning rates.** Mean ( $\pm$  SE) nesting provisioning rates (a) control (tanager) versus (b) nest predator (jay) presentations for the pre-stimulus versus stimulus presentation periods. Each point represents a different species. (Source: [Ghalambor, Peluc, & Martin 2013](#))

A second important factor that reduces current fitness for parents is missed opportunity cost, or the sacrifice that an individual makes by not engaging in a different behavior that may enhance current fitness. For example, by guarding eggs, a male cannot search for new mates. Let's see one example of opportunity costs in frogs that helps to explain variation in parental care among individuals and provides a second test of parent-offspring conflict theory.

## FEATURED RESEARCH Egg guarding and opportunity costs of parental care in frogs

For many insects, fish, and amphibians, egg attendance is an important aspect of parental care. One parent remains near the eggs to protect them from predators and remove infected or dead eggs. Experimental removal of the guarding parent typically leads to reduced hatch success, showing the benefits of offspring defense as a form of parental care. Just as we saw in egg carrying, the amount or intensity of egg guarding varies among individuals within a population. For example, in big-thumbed frogs (*Kurixalus eiffingeri*), some males attend eggs nearly

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within a population. For example, in big-thumbed frogs (*Kurixalus eiffingeri*), some males attend eggs nearly 100% of the time until they hatch, whereas others rarely stay near eggs to guard them (Figure 14.9). Wei-Chun Cheng and Yeong-Choy Kam investigated this variation ([Cheng & Kam 2010](#)), asking the question: If egg attendance increases hatch success, why don't all males attend eggs at a high level?



**FIGURE 14.9. Big-thumbed frog.** Males display egg-guarding behavior.

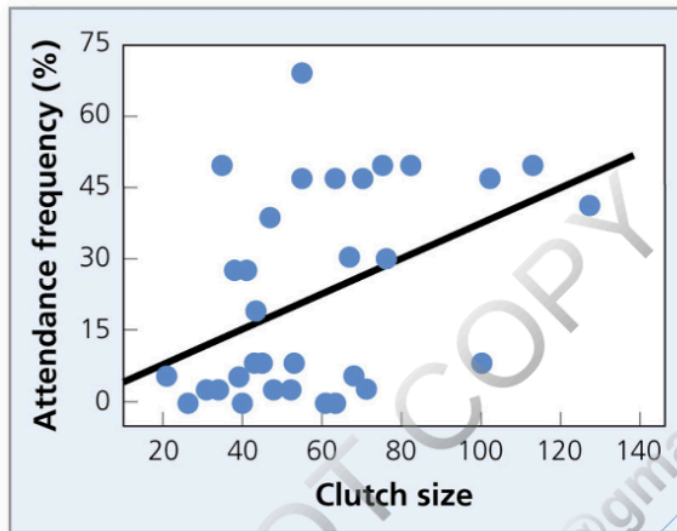
This species, native to Taiwan, has an extended breeding period that lasts from February through August. During mating, the pair engages in amplexus: a male grasps a female. Males can then fertilize the eggs she deposits in water-filled bamboo stumps or tree holes, making it easy to identify the eggs that a male has fertilized.

Males guarding eggs were captured and uniquely marked using a waistband with a small numbered tag. Each night for six days, 38 egg masses were observed six times to determine whether the male was attending the eggs. The research team also noted any egg mortality by counting the number of eggs still in the nest.

Daily egg mortality was negatively correlated with attendance, demonstrating the benefits of male parental care. Male attendance was also positively correlated with egg clutch size: males were more likely to attend larger clutches (Figure 14.10). Why do males with small egg clutches spend less time attending them? The researchers proposed that such males are instead searching for additional mating opportunities to increase their fitness. Time spent attending eggs reduces the ability of a male to search out and mate with additional females. A male with a small clutch of 20 to 30 eggs has less to lose by allocating little time to parental care and more to gain by seeking out other mates. In contrast, males that have already fertilized a large clutch of over 100 eggs can best enhance their fitness by protecting them until they hatch. So here, variation in clutch size and our understanding of life history trade-offs and opportunity costs can explain variation in parental care among males.

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**FIGURE 14.10. Egg attendance in frogs.** Males with large clutches had higher attendance frequency than males with small clutches. (Source: [Cheng & Kam 2010](#))

In these examples, increased costs to parents led to a reduction in the level of care for current offspring, as predicted by parent-offspring conflict theory. The theory also predicts a fitness trade-off between current and future reproduction, stating that parents that invest more in their current offspring will have higher current reproductive success but also reduced future reproductive success. Let's examine this prediction by first considering parental care and reproduction in insects.

## FEATURED RESEARCH Current versus future reproduction in treehoppers

One way to test parent-offspring conflict theory is to examine how variation in individual parental care affects both current and future offspring. Andrew Zink tested the theory by studying a common species of treehopper, *Publilia concava*, at a site in New York ([Figure 14.11](#)) ([Zink 2003](#)). In these small, plant-feeding insects, females select a host plant and lay eggs on the underside of mature leaves. Parental care takes the form of egg guarding as females protect their offspring from predators such as mites. In this species, there is tremendous variation among females in guarding behavior: some guard their eggs for three or more weeks until nymphs hatch, whereas others spend no time at all caring for their eggs. There is also variation in the number and size of egg clutches a female can produce in one reproductive season. Are these patterns related?

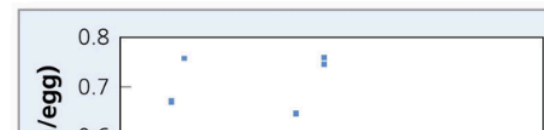


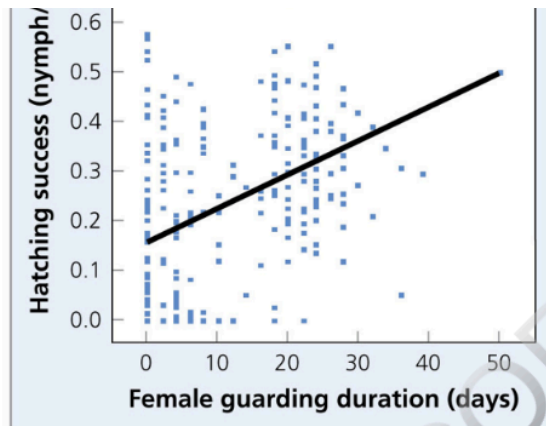
**FIGURE 14.11. Treehopper.** Treehoppers feed on host plants and lay eggs on the underside of leaves.

Zink examined how parental care affected both current and future reproduction of individual females. Based on the existence of a trade-off between current and future reproduction, he made two predictions: (1) egg guarding will increase egg survival and thus enhance current reproduction, and (2) increased parental care (guarding) will decrease future reproductive success.

Zink uniquely marked females with four small dots of colored paint. Because females are generally faithful to individual plants, he could follow their behavior and the fate of egg clutches through repeated visits. For each egg mass deposited by a female, he measured its size to estimate the number of eggs and checked them every two days until the nymphs hatched. At each check, he also recorded whether the female was present (guarding the eggs) or had abandoned them. Hatching success (an estimate of fitness) was calculated as the number of nymphs observed on the leaf divided by the number of eggs estimated in a clutch.

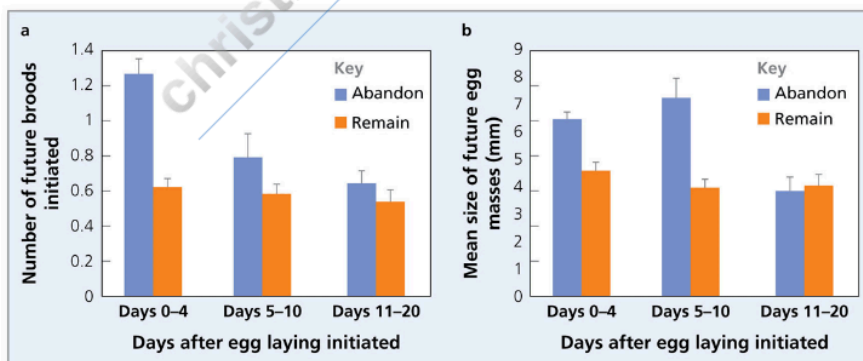
Zink found that about half the females abandoned their eggs within a few days of their deposition, while the rest remained to guard them for more than three weeks. He also found a positive correlation between the duration of egg guarding and hatching success ([Figure 14.12](#)), demonstrating a benefit of care for current reproduction that supports the first prediction. Although the correlation might be due to successful female defense, it might also result from females abandoning clutches that are damaged or otherwise unviable.





**FIGURE 14.12. Effect of egg guarding in treehoppers.** There is a positive correlation between the number of days a female guards eggs and the eggs' hatching success. Each point represents one female. (Source: Zink 2003)

To test these alternatives, Zink conducted a removal experiment. He identified 194 plants that contained egg clutches that were similar in size. In half—deemed “removal treatment” clutches—the female was removed to reduce the level of parental care that offspring received. In the other half, clutches were not manipulated (female not removed; the control) and so received a higher level of care. Zink observed that hatch success was significantly higher in controls, providing more evidence that parental care enhances current reproduction. Is there a cost of care in terms of future reproduction? Yes. Females that provided more than ten days of care for their first clutch were less likely to initiate a second clutch than were females that abandoned their first clutch in the first ten days. Another way to characterize the trade-off involved in the cost of care is to examine the benefit of providing little care: females that abandoned their first clutch early laid larger second clutches than females that provided greater care for their first clutch (Figure 14.13). As such, these data support both predictions of the parent-offspring conflict theory.



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**FIGURE 14.13. Egg guarding and future reproduction in treehoppers.** (a) Mean (+ SE) number of future broods initiated and (b) size of future egg masses. Females that abandoned a clutch (blue bars) as opposed to remaining with their eggs (orange bars) in the first ten days after egg laying initiated more future broods of larger size. (Source: Zink 2003)

In this example, Zink relied in part on natural variation in parental care among females to test parent-offspring conflict theory. An alternative approach is to experimentally manipulate the costs of providing care to current offspring and examine the effect on future fitness, as we see in the next example.

#### Video: Treehopper reproductive behavior

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## FEATURED RESEARCH Incubation of eider eggs as a trade-off

In birds, egg incubation is an important component of chick development. Adults sit on eggs and transfer heat to them through their brood patch, a featherless area on the belly that is well vascularized for heat transfer to eggs. This behavior can be critical when the ambient temperature is low.

Sveinn Hanssen and colleagues were interested in how current incubation costs affect future reproduction in the common eider (*Somateria mollissima*) (Hanssen et al. 2005). Eiders are large sea ducks that live primarily along the cold northern coasts of Europe and North America. Females normally lay a clutch of three to six eggs with four to five eggs on average. They incubate the clutch alone without the help of their mate. During the two-week incubation period, females do not leave the nest to eat and so typically lose up to 40% of their body mass—a large parental investment indeed! Assuming that six eggs take more energy to warm than three, Hanssen and colleagues predicted that incubating larger clutches should lead to a greater loss in body mass. Because the eider is a long-lived bird (living up to 12 years), the research team could also examine how mass loss affected future reproduction (Scientific Process 14.2).

### SCIENTIFIC PROCESS 14.2

#### Parental care costs in eiders



Research Question: Does egg incubation affect future reproduction?

### Hypothesis:

There is a trade-off between current incubation costs and future reproduction.

### Prediction:

Individuals with large clutches will pay high incubation costs and experience lower reproductive fitness in the future compared to those with small clutches.

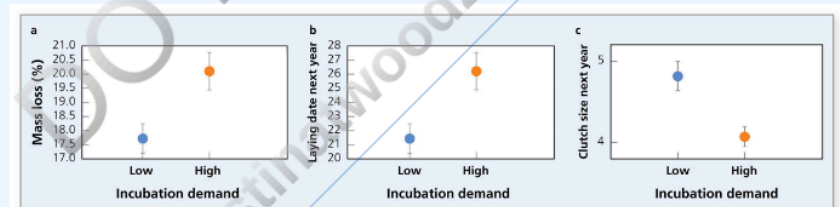
### Methods:

The researchers:

- Manipulated the clutch size of uniquely marked females (either decreasing the clutch to three eggs or increasing it to six eggs)
- Recorded the body mass of each female at the beginning and end of the 15-day incubation period
- Recorded egg-laying date and clutch size for each female in the following year

### Results:

Females with high incubation costs lost more mass and had later egg-laying dates and smaller clutches in the next breeding season than those with low incubation costs.



**FIGURE 1.** Incubation costs. Mean ( $\pm$  SE) effects of high and low incubation costs on (a) body mass loss, (b) laying date the next year, and (c) clutch size the next year in female common eiders. (Source: Hanssen et al. 2005)

### Conclusion:

High incubation costs in one year reduce reproductive fitness in the next breeding season.

### Evaluate



## Evaluate

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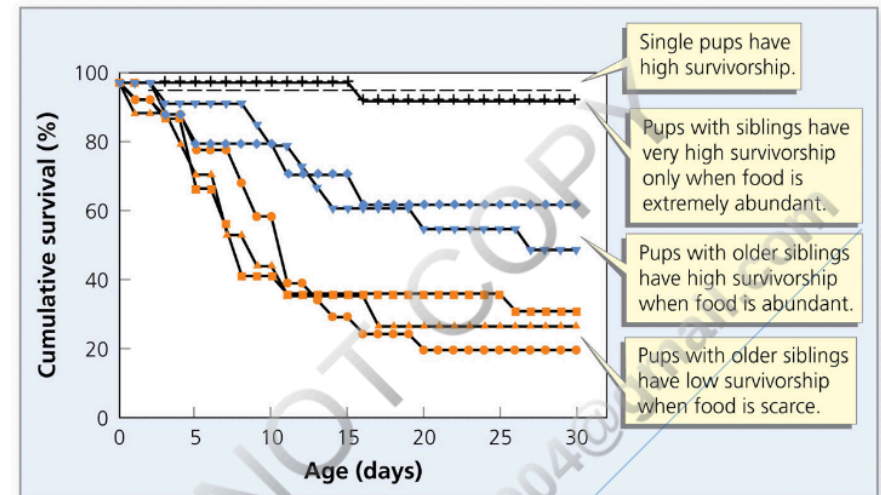
What is another potential fitness cost associated with high incubation costs?

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advantage of the rich food supply. The production of “extra” offspring allows parents to increase their reproductive output. In contrast, in years of low food availability, mortality of the younger pup is high. Conservation biologists are taking advantage of this relationship to help boost populations of endangered species ([Applying the Concepts 14.3](#)).



**FIGURE 14.15. Fur seal pup survival.** Cumulative survival of single pups was high in all years (horizontal dashed line). The survival of pups with older siblings was related to water temperature, which was an index of food availability. In cold-water years with high food availability (blue), survival was high. In warm-water years with low food availability (orange), survival was low. (Source: [Trillmich & Wolf 2008](#))

### APPLYING THE CONCEPTS 14.3

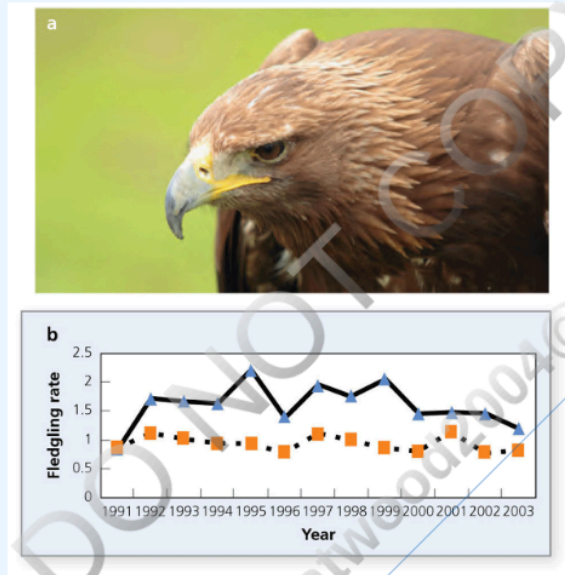
#### Food supplementation reduces brood reduction in endangered eagles

Brood reduction is common in many birds of prey, such as hawks and eagles. One species that exhibits brood reduction is the endangered Spanish imperial eagle (*Aquila adalberti*). Females lay clutches of one to four eggs over a one-week period, but mortality of chicks is high after the first offspring, so typically only about one chick fledges. The Spanish imperial eagle is one of the rarest birds of prey in the world, with a population size of around 200 breeding pairs. Given brood reduction in the species, conservation biologists have considered two strategies to increase population size. First, biologists can remove second-hatched chicks and place them in other nests or hand-raise them and release them into the wild as juveniles ([Meyburg 1978](#)). However, these procedures disturb the nest, are costly, and often are ineffective. An alternative is to provide supplemental food to adults with two chicks.

Luis González and colleagues tested the prediction that supplemental feeding would reduce brood reduction in Spanish imperial eagles in western Spain ([González et al. 2006](#)). For 12

brood reduction in Spanish imperial eagles in western Spain (González et al. 2006). For 13 years, they provided European rabbit carcasses to 22 nests containing more than one chick. Another 37 nests with multiple chicks served as controls.

Supplemental feeding increased chick survival almost every year (Figure 1). In most years, almost twice as many chicks fledged in nests that received supplemental food than did in control nests. The research team concluded that Spanish eagle reproduction is food-limited, and that population growth can be enhanced by supplemental feeding. This management tool is cheap, nonintrusive, and effective.



**FIGURE 1.** Effect of food supplementation on fledgling success. (a) Spanish imperial eagle. (b) Fledgling rate (number of fledglings per pair) for food-supplemented (blue triangle) and control (orange box) nests in different years. (Source: González et al. 2006)

Why do parents produce more offspring than they can care for? If they didn't, there would be no need for brood reduction. First, "extra" offspring provide some "insurance": if the first-born offspring dies, a second will still be alive. Second, parents do not have information on how much food will be available in the future, when offspring demand for food is high. If the environment contains abundant food, a parent may be able to successfully increase its reproductive fitness for the year. If the benefit of producing an extra offspring is greater than the cost, we can predict that selection can act such that parents will produce "extra" siblings and brood reduction will occur in years of low resources. In this light, brood reduction allows parents to adjust their reproductive effort to environmental conditions.

In the previous examples, we have seen how the fitness trade-off between current and future reproduction, which forms the basis of parent-offspring conflict theory, helps explain variation in parental care both among individuals and to offspring. This trade-off is driven by the substantial cost to parents of caring for their offspring. Next, we examine how selection can favor individuals that reduce such costs via brood parasitism.

## 14.4 Brood parasitism reduces the cost of parental care and can result in a coevolutionary arms race

### Learning Objectives

After reading this section, you should be able to

- explain the benefits and costs of brood parasitism and
- describe how intra- and inter-specific brood parasitism can evolve.

Throughout this chapter, we have seen that parental care is costly and that the costs are often borne disproportionately by females—a situation that can favor the evolution of behaviors that reduce costs. One way to reduce the cost of parental care is for a female to lay her eggs in the nest of another female, called a “host,” a behavior known as **brood parasitism**. The benefit of this behavior is reduced parental care, which can then result in enhanced reproductive success for the brood parasite. Although the benefit of parasitism is clear, it does entail some risk: a parasitized female may reject the added eggs or chicks, an outcome that will not increase fitness for the female parasite. How can a brood parasite reduce the likelihood of egg rejection?

The simplest way to avoid egg rejection is to parasitize conspecifics by laying eggs in the nests of other females of the same species. Rejection by the host will be difficult because the eggs of conspecific females look similar. Conspecific brood parasitism is common in birds, with examples from over 200 species (Yom-Tov 2001), and also occurs in fish and insects (Wisenden 1999; Tallamy 2005).

To examine the benefits of conspecific brood parasitism, we might envision three reproductive tactics that a female could use (Sorenson 1991): (1) lay all eggs in her own nest (nonparasite); (2) lay all eggs in the nests of other females (pure parasite); and (3) lay some eggs in her own nest and some in the nests of others (a mixed strategy of nesting and parasitizing).

Let's examine one study that attempted to quantify the fitness of these three reproductive strategies.

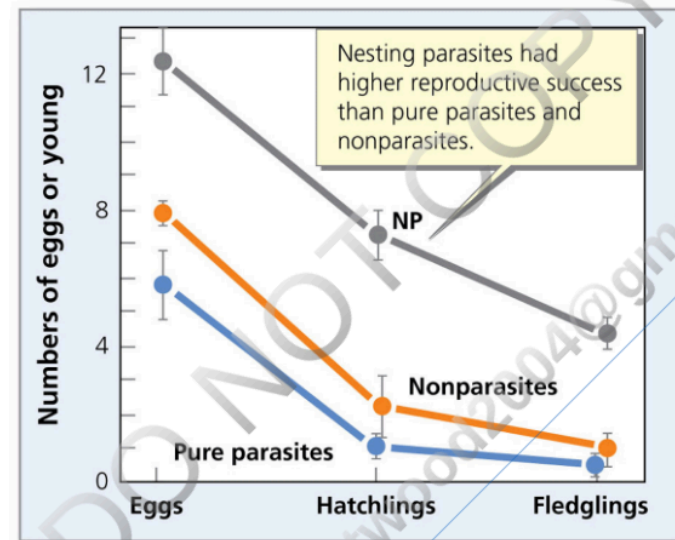
### FEATURED RESEARCH Conspecific brood parasitism in ducks

Matti Åhlund and Malte Andersson examined the prevalence of conspecific brood parasitism in a population of marked female goldeneye ducks (*Bucephala clangula*) nesting in Sweden (Åhlund & Andersson 2001). They used egg albumin protein fingerprinting to identify the maternity of eggs and hatchlings within a nest. Albumin is deposited by the female into the egg and contains over a dozen proteins. Many of these proteins exhibit genetic polymorphisms, so there is much genetic variation among females. Therefore, each female exhibits a unique

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polymorphisms, so there is much genetic variation among females. Therefore, each female exhibits a unique protein-banding pattern, allowing researchers to identify the maternity of different eggs (Andersson & Åhlund 2000). Nests were monitored regularly to determine egg laying, and there was no evidence of egg removal by any female. All chicks were marked with numbered tags, and their survival was recorded over four weeks.

The researchers found that all three strategies existed in the population studied, but females that used the mixed nesting and parasitizing tactic had the highest reproductive success. These females laid about 50% more eggs than nonparasites or pure parasites (Figure 14.16), and the eggs they laid in host nests survived equally as well as nonparasite eggs, indicating that they were not rejected.



**FIGURE 14.16. Brood parasitism in ducks.** Mean ( $\pm$  SE) number of eggs or young for females classified as pure parasites (blue), nonparasites (orange), or nesting parasites (NP, gray). The latter laid the most eggs and had the highest number of hatchlings and fledglings survive. (Source: Åhlund & Andersson 2001)

The researchers observed variation in the reproductive tactics used by a female across years and found no evidence that nesting parasites suffered lower survival or reproduction in subsequent years, despite laying more eggs. Why this occurred is unclear, and so further work is required to understand the reproductive tactics of conspecific brood parasites in this population. Nonetheless, one factor that likely favors the evolution of brood parasitism in this and other species is its minimization of the costs associated with parental care.

### Interspecific brood parasitism and coevolution

While many species, like goldeneye ducks, lay eggs in the nests of conspecifics, some brood parasites lay their eggs in the nests of other species and are thus known as **interspecific brood parasites**. About 1% of bird species

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eggs in the nests of other species and are thus known as **interspecific brood parasites**. About 1% of bird species, including many cuckoos and cowbirds, are obligate brood parasites: they *only* lay eggs in the nests of other species, thus avoiding all costs of parental care. This behavior can greatly enhance the fitness of the brood parasite. Female brown-headed cowbirds (*Molothrus ater*) can lay as many as 40 eggs in the nests of hosts during a single reproductive season, all without the cost of parental care. Brood parasitism has a correspondingly negative effect on host fitness; for example, common cuckoo chicks (*Cuculus canorus*) kill host offspring. Similarly, cowbird chicks are competitively dominant to host chicks, and so the parasite receives a disproportionate share of the care (food) provided by the host parent.

**Video: Large oriental cuckoo chick (brood parasite) being fed by much smaller parent bird**

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Given the fitness costs of brood parasitism, selection should favor hosts that can discriminate their own eggs from those of a parasite so that the latter can be rejected (i.e., removed from the nest). Indeed, egg rejection behavior has evolved in many species that co-occur with brood parasites (Davies 1999).

**Video: American robin rejects cowbird (parasite) egg**

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When hosts evolve this ability, selection can favor brood parasites that produce eggs similar in appearance to host eggs, making discrimination more difficult. Many brood parasites, including the common cuckoo, have evolved traits that reduce the likelihood of egg rejection by a host, including the production of eggs that match the size, color, and shape of host eggs so that it is difficult for the host to distinguish its eggs from that of the parasite (Figure 14.17) (Stokke, Moksnes, & Røskaft 2005). Such a coevolutionary arms race, driven by the costs of parental care, should continue to affect the evolution of both egg rejection behavior and hosts' discrimination ability.





**FIGURE 14.17. Parasitic egg in nest.** A cuckoo egg (the largest) in a redstart (*Phoenicurus phoenicurus*) nest. Note the similarity in the egg coloration.

Not all species that live with brood parasites reject their eggs. For example, brown-headed cowbirds commonly parasitize dozens of species. About 24 of these regularly reject cowbird eggs, but over 30 rarely do so. Why not?

The evolutionary lag hypothesis states that species without an evolutionary history with brown-headed cowbirds are more likely to be egg acceptors than those that have a longer evolutionary history with the species. The geographic range of brown-headed cowbirds has expanded greatly over time. This species was historically restricted to open habitats in the Great Plains of North America but now occurs throughout the continent as a result of logging that has cleared forest habitat. This range expansion has increased the availability of new host species that have no evolutionary history with brown-headed cowbirds. Such species are more likely to be egg acceptors than are those that have a longer evolutionary history with brown-headed cowbirds.

Another hypothesis, the bill size hypothesis, states that only species with sufficiently large bills can successfully remove cowbird eggs. This is because most egg rejection requires a host to grasp and lift the cowbird egg with the bill. This hypothesis predicts that species with large bills are more likely to be rejectors than are those with small bills. Next, we examine a study designed to test these hypotheses.

## FEATURED RESEARCH Acceptance or rejection of brown-headed cowbird eggs by hosts

Brian Peer and Spencer Sealy tested the evolutionary lag and bill size hypotheses by conducting a comparative analysis of brown-headed cowbird hosts (Peer & Sealy 2004). They began by identifying 26 host species known to reject cowbird eggs at a high frequency and 32 acceptor species. From these they identified 12 pairs of closely related species that are known to be parasitized by brown-headed cowbirds and that differ in egg rejection rate. The research team deemed a species to have a long evolutionary history with brown-headed cowbirds if its historic geographic range overlapped with that of cowbirds and if it nested in open habitats. Bill sizes (length) were obtained for each species from the literature, which was supplemented with measurements of museum

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Analysis of the data supported both hypotheses. For the five species pairs that differed in evolutionary history, the species with the shorter history was always an egg acceptor, while the species with the longer history was always a rejector. In the seven species pairs that differed significantly in bill size, the species with the longer bill was always a rejector, while the species with the shorter bill was always an acceptor. Thus, both length of time in contact with a brood parasite and bill size explain variation in egg rejection behavior in North American host species.

Throughout this chapter we have seen that parental care is costly but can enhance fitness by increasing the survivorship of young. How are parental care behaviors regulated? We examine this question next.

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## 14.5 Hormones regulate parental care

### Learning Objectives

After reading this section, you should be able to

- describe a proximate mechanism for the initiation of parental care in vertebrates and
- explain how juvenile hormones may trigger parental care in invertebrates.

Many adults exhibit a radical change in behavior over the course of the reproductive season. Before mating, individuals concentrate on finding and attracting a mate. As the reproductive season progresses and more individuals mate successfully, mating behavior declines and parental care increases. For example, birds switch from mating displays to nest building, egg incubation, and then chick feeding. Female mammals undergo a change in physiology to begin lactation. What initiates and regulates these changes?

In mammals, steroid hormones such as estradiol and progesterone vary with pregnancy and can strongly affect courtship and reproductive behavior. The peptide hormone **prolactin**, which is involved in milk synthesis, rises during pregnancy and then falls when offspring are weaned (Zarrow, Gandelman, & Denenberg 1971). It is synthesized in and secreted from specialized cells in the anterior pituitary gland. Does prolactin affect parental care?

## FEATURED RESEARCH Prolactin and maternal care in rats

Robert Bridges and colleagues conducted a series of classic experiments to examine the effect of prolactin, estradiol, and progesterone on maternal behavior in rats (Bridges et al. 1990). They manipulated prolactin levels in female rats that had never given birth. To set up the experiment, they first treated all individuals with the drug bromocriptine to suppress endogenous prolactin secretion so that the rats could not produce their own prolactin. The research team also removed each rat's ovaries to control the levels of other hormones and inserted a cannula—a small tube—into the brain to administer hormones directly into the central nervous system. All females were “primed” with progesterone and estradiol to mimic the changes in these steroid concentrations that occur in pregnant rats. The researchers then examined the behavior of females treated with different levels of either prolactin or a sodium chloride–sodium bicarbonate control. Next, they placed three unrelated pups into the home cage of each female. Over a period of six days, Bridges and colleagues recorded three aspects of parental care: latency to contact the pups, whether pups were retrieved and carried to the nest, and instances of crouching behavior (huddling over pups to keep them warm) (Figure 14.18).







**FIGURE 14.18. Female rat with young.** Females huddle over pups to keep them warm.

There was a rapid increase in maternal behavior in treatment females by Day 3. Females treated with prolactin displayed significantly higher levels of parental care behavior than did controls ([Figure 14.19](#)). In follow-up experiments, the research team examined whether prolactin could stimulate maternal behavior without the steroid regimen. The experimental procedures followed were identical to those of the prior study, except that females were not primed with progesterone and estradiol. Without the steroid hormones, females did not display maternal behavior ([Figure 14.19](#)). To determine the action site of prolactin, the researchers injected prolactin subcutaneously but found no difference in maternal behavior compared to

## CHAPTER SUMMARY AND BEYOND

Species differ in life history traits, which can explain the variation in parental care across species: those with a long life span or well-developed offspring at birth tend to provide high levels of parental care. Research has focused on understanding the evolution of parental care in different groups ([Royle, Smiseth, & Kölliker 2012](#)). For instance, parental care in birds appears to have evolved first in their extinct ancestors, the dinosaurs ([Varricchio et al. 2009](#)). Other work has examined the evolution of trade-offs involving parental care and other life history traits in insects ([Wong, Meunier, & Kölliker 2013](#); [Gilbert & Manica 2015](#)) and fish ([Kolm & Ahnesjö 2005](#)). In addition, males and females differ in the fitness benefits they obtain from providing parental care because of the differing costs of care, particularly in terms of the certainty of relatedness to offspring. For most species, and especially for species with internal fertilization, females are more certain of their offspring than are males. This difference favors greater levels of parental care by females. Reduced parental care allows individuals to seek additional sexual partners or allocate more energy to future reproduction.

Adults provide care to increase survivorship of their offspring, but doing so reduces their future reproductive fitness, resulting in a trade-off between allocating care effort to current offspring and allocating such effort to future offspring. This trade-off explains variation in care among individuals, and ongoing work examines the mediating effect of hormones in this relationship ([McGlothlin, Jawor, & Ketterson 2007](#); [Rosvall 2013](#)). This trade-off also explains why parents often provide unequal care to siblings and how unequal care can result in brood reduction. The high costs of parental care help explain the evolution of intra- and interspecific brood parasitism. [Feeney, Welbergen, & Langmore \(2012\)](#) provide an extensive review of this subject.

Prolactin is an important hormone that regulates parental care. It initiates lactation and parental care behavior in mammals and also is involved in stimulating parental care in birds ([Rilling & Young 2014](#); [Angelier, Wingfield, Tartu, & Chastel 2016](#)). Prolactin may also be an important factor in the development of paternal care in fish ([Schradin & Anzenberger 1999](#); [Bender, Taborsky, & Power 2008](#)). In insects, juvenile hormone production is often negatively associated with parental care behaviors. [Mas and Kölliker \(2008\)](#) have reviewed work on the physiological aspects of parental care in insects and highlight recent work on chemical communication between mother and offspring that affects the level of care provided.

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# CHAPTER 13

## Mating Systems

Shawn E Nordell      Thomas J Valone  
Washington University in St. Louis      Saint Louis University

### Concepts

- 13.1 [Sexual conflict and environmental conditions affect the evolution of mating systems](#)
- 13.2 [Biparental care favors the evolution of monogamy](#)
- 13.3 [Polygyny and polyandry evolve when one sex can defend multiple mates or the resources they seek](#)
- 13.4 [The presence of social associations distinguishes polygynandry from promiscuity](#)
- 13.5 [Social and genetic mating systems differ when extra-pair mating occurs](#)

### Features

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	13.2 <a href="#">Monogamy in snapping shrimp</a>
Applying the Concepts	13.1 <a href="#">Mating systems and conservation translocation programs</a>
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Quantitative Reasoning	13.1 <a href="#">Mating success of male red-backed fairy-wrens</a>

When we are in Arizona, we enjoy taking walks in the desert, especially when animals are busy with the business of reproduction. It is easy to hear and see cactus wrens (*Campylorhynchus brunneicapillus*), the largest wren in North America. A male and female pair up, defend a territory, and raise their offspring together. Hummingbirds are everywhere. Males possess bright iridescent plumage and engage in aerial displays near a female sitting in a tree. Some males may mate with several females, while others fail to find a mate. Each female builds a nest, incubates the eggs, and feeds the young without aid from a male. And it is always nice to see desert spiny lizards (Figure 13.1). Males engage in aggressive contests as they defend their territories, and those that successfully defend a high-quality territory can often mate with several females.

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incubates the eggs, and feeds the young without aid from a male. And it is always nice to see desert spiny lizards (*Sceloporus magister*) (Figure 13.1). Males engage in aggressive contests as they defend their territories, and those that successfully defend a high-quality territory can often mate with several females.



FIGURE 13.1. Desert spiny lizard. Males defend territories during the mating season.

Wrens, hummingbirds, and lizards differ in the social associations and number of mates they have during a breeding season, and they represent a few of the mating systems that exist. In this chapter, we review mating system diversity and examine theories to explain such variation. We also discuss how social mating systems that are based on behavioral association differ from genetic mating systems, which are based on genetic parentage.

### Video: Male desert spiny lizard doing pushup display

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## 13.1 Sexual conflict and environmental conditions affect the evolution of mating systems

### Learning Objectives

After reading this section, you should be able to

- distinguish monogamy, polygyny, polyandry, polygynandry, and promiscuity;
- use the Emlen and Oring model to predict how variation in sexual conflict and resource abundance affect a mating system; and
- differentiate between resource defense and female defense polygyny.

Animals exhibit different **mating systems**—the social associations and number of sexual partners an individual has during a breeding season. [Table 13.1](#) summarizes differences among the five mating systems: monogamy, polygyny, polyandry, polygynandry, and promiscuity. In some mating systems, individuals live in close association with one another during the breeding season and are said to form a pair bond. However, pair bonds are far from universal, and an individual's number of mates and types of social association range widely across taxa. It is important to emphasize that these mating systems are defined within one reproductive season. In many species, individuals mate with a different partner in successive breeding seasons, even if they are, for instance, monogamous within a single season.

**TABLE 13.1 Mating systems.** Mating systems differ in the number of mating partners each sex has during one breeding season.

Mating System	Number of Females	Number of Males
Monogamy	1	1
Polygyny	More than 1	1
Polyandry	1	More than 1
Polygynandry, or plural breeding (mating occurs within social groups)	More than 1	More than 1
Promiscuity (mating is not restricted to specific social associations)	More than 1	More than 1

Over the past few decades, our understanding of animal mating systems has changed dramatically. In the past, we assumed that each species had a characteristic mating system. Today, we understand that species, populations, and even individuals can exhibit tremendous variation in their mating systems. For instance, four mating systems have been observed in single populations of both dunnocks (*Prunella modularis*), an insectivorous bird found in Europe



(Davies & Lundberg 1984), and Milne-Edwards' sifakas (*Propithecus edwardsi*), a social primate that lives in Madagascar (Pochron & Wright 2003). Although these examples are extreme, we do often find more than one type of mating system within a species. To understand why, we need to consider the factors that influence the evolution of mating systems. As we see next, these factors involve the reproductive decisions of males and females. Such decisions are affected by their fitness benefits and costs, which in turn vary with environmental conditions.

## The evolution of mating systems

Stephen Emlen and Lewis Oring argued that mating systems can be understood by examining two factors. One is evolutionary: **sexual conflict**, or the differential selection on males and females to maximize their fitness. The other factor is ecological: the ways in which resource limitation and distribution affect fitness benefits and costs for each sex (Emlen & Oring 1977). We need to examine these factors together to understand the variability in mating systems.

Emlen and Oring's model assumes that for a female, fitness will often be more strongly limited by the resources she can obtain to invest in offspring than by the number of her sexual partners (Bateman 1948; Emlen & Oring 1977). This idea follows from the assumption that females typically invest more energy in offspring than males do. First, because of their relatively large size, eggs should require more energy to produce than sperm. For example, female birds and reptiles may invest up to 50% of their body mass in production of a single clutch of eggs (e.g., Vitt & Price 1982; Monaghan & Nager 1997). Second, in many species, females expend more energy on parental care (e.g., incubation, feeding, and defense) than do males, as we will see in Chapter 14. In addition, most females can obtain sufficient sperm from a single male to fertilize all her eggs for one reproductive event. In contrast, for a male, fitness is most strongly affected by the number of sexual partners he obtains. The more partners, the higher his fitness. This difference sets the stage for sexual conflict.

Emlen and Oring suggested that for a female, selection will favor a mating system that provides the greatest access to resources. If the female's sexual partner provides high levels of resources to the young, such as a high-quality territory and a great deal of parental care, **monogamy**—one male with one female—will be favored. If multiple males all provide care to the female's offspring, **polyandry**—one female with multiple males—will be favored. In contrast, for males, selection will favor **polygyny**—one male with multiple females—when males that mate with multiple partners have higher fitness than those that mate with a single female (see Table 13.1). If sexual conflict does not exist because care from both parents is required to raise offspring successfully, as occurs in many birds (e.g., Black 1996), selection will favor monogamy and **biparental care**. Emlen and Oring suggested that this system might often be favored in resource-poor environments or when resources are difficult to obtain. Biparental care and monogamy might also be favored when predation on unattended young is high.

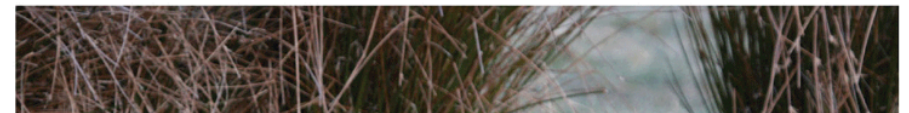
When biparental care is not required and parental care is female biased, selection will favor the evolution of polygyny. Polygyny is predicted to evolve when environmental conditions lead to the aggregation of females, because such aggregations are more easily defended by a male from rivals. Two factors can promote female aggregation. First, females may aggregate for reasons other than reproduction. For instance, aggregations of females may experience lower predation risk than solitary females, or a group of females may more successfully avoid harassment from males (e.g., Dada, Pilastro, & Bisazza 2005). In such cases, **female defense polygyny** occurs when males monopolize aggregations of females directly (Figure 13.2). The second factor that can lead to aggregation of females is the distribution of resources in the environment. If the resources required by females are

clumped, males can monopolize females by defending territories with large amounts of such resources. **Resource defense polygyny** occurs when males defend territories rich in the resources that are used by and attract multiple females. A male then mates with the females that remain near the resources he defends.



**FIGURE 13.2. Female defense polygyny.** A male (a) impala (*Aepyceros melampus*) and (b) South American sea lion (*Otaria byronia*) defend their harem of females.

Sometimes, however, resources and females may be more uniformly distributed in an environment, rather than clumped. Alternatively, resources may be too unpredictable in space or time, making them costly to defend. If it is too costly for males to defend resources or females successfully, potential mates must seek each other out, which can involve high energetic and predation costs. One way to reduce these costs is for males to settle in fixed locations, called leks, and then display to females there (Figure 13.3). Leks have evolved in many taxa, and males typically form dominance hierarchies within the lek, with dominant males occupying the most preferred, often central, locations. Such males typically mate with several females, a mating system that Emlen and Oring called **male dominance polygyny**. Males on leks can benefit as a result of reduced predation risk, and such aggregations may be more attractive to females than a single male (Alatalo et al. 1992), thereby increasing encounters with them. Females, too, can benefit from the existence of leks, because their existence reduces the time required to search for a mate: females can quickly assess the relative quality of different males on a lek to find the best option.





**FIGURE 13.3. Lek.** Male black grouse (*Tetrao tetrix*) display on a lek.

In a polyandrous mating system, one female associates and mates with multiple males. Emlen and Oring suggest that polyandry can evolve when it is advantageous to both sexes that females be freed from providing parental care, making parental care male biased. One possible situation that might produce a polyandrous system is one in which there is very high predation on offspring. If many offspring are lost to predators, both sexes can benefit if a female can quickly reproduce again. However, recall that egg production is costly. If a male provides more care, a female can provide less and thus feed more often to quickly replenish her energy stores for reproduction in the event that current offspring do not survive. Once males provide high levels of care and females are able to lay multiple clutches quickly, selection can favor females that mate with multiple males and lay a clutch of eggs that is then tended by each one.

#### Video: Black grouse lek with males displaying

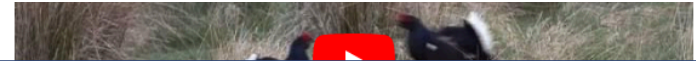
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Video: Black grouse lek with males displaying



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Both **polygyny** (or plural breeding) and **promiscuity** involve multiple mating partners for each sex but differ in regard to social associations: social associations are found in polygyny, but not in promiscuity (see [Table 13.1](#)). Polygyny is rare but does occur in some social species, and particularly in mammals that defend a territory from other such groups. For example, African lions (*Panthera leo*) live in social groups, which facilitates hunting success ([Figure 13.4](#)). A pride consists of two or more adult males, which are often relatives, and up to nine adult females. Males defend their females, and multiple males mate with multiple females ([Packer et al. 1991](#)).



**FIGURE 13.4. African lions.** Multiple male lions defend and mate with multiple females, a polygynous (plural) breeding system.

Promiscuity, on the other hand, should evolve when the benefits of social living are low. Both females and males



Promiscuity, on the other hand, should evolve when the benefits of social living are low. Both females and males are then solitary, and pair-bond formation provides no fitness benefits to either sex. Conditions also favor this system's evolution when the defense of mates or resources is uneconomical, as might occur when population density is high or when it is too costly for males to aggregate on leks, as in high predation risk conditions. Such a system might also occur when individuals cannot afford to forgo feeding to spend time on a lek.

In sum, Emlen and Oring's model suggests that mating system variation can be understood by examining (1) the competing interests of the sexes in attempting to maximize their fitness and (2) how environmental conditions affect the benefits and costs of resource defense and of different mating behaviors for each sex (Figure 13.5). Clearly, mating systems and parental care behavior have co-evolved. In this chapter, we'll see how the model proposed by Emlen and Oring helps to explain the evolution of, and variation in, mating systems. We cover parental care in the next chapter.

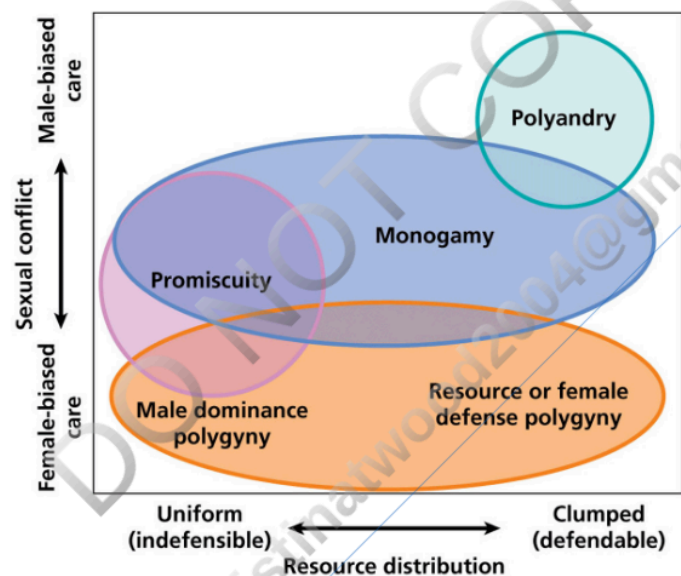


FIGURE 13.5. Emlen and Oring's model. Mating systems are the result of the interaction between sexual conflict and resource distribution.

## FEATURED RESEARCH Mating systems in reed warblers

One way to evaluate the Emlen and Oring model is to use the comparative approach to examine a group of related species that exhibit different mating systems. The model allows us to predict, for example, how variation in resource abundance should affect a mating system. In resource-poor environments, biparental care will often be required to raise offspring successfully, and so monogamy should be favored. When resources are more abundant, biparental care will be less essential, and so polygyny or perhaps promiscuity should be favored.

Bernd Leisler, Hans Winkler, and Michael Wink examined these predictions for the evolution of mating systems in 17 species of acrocephaline reed warblers (Leisler, Winkler, & Wink 2002). These insectivorous birds are widely distributed throughout the Old World in a variety of marshy and shrubby habitats. All female reed warblers provide more parental care than males through behaviors such as egg incubation and food delivery to young, but the level of male care varies across species. Most species are monogamous, but several are polygynous, and one exhibits promiscuity (Figure 13.6). Leisler and colleagues used the comparative method to address two research questions. First, how does habitat quality—defined as the amount of food resources—correlate with mating system? Second, how are habitat quality and mating system related to the level of male care?

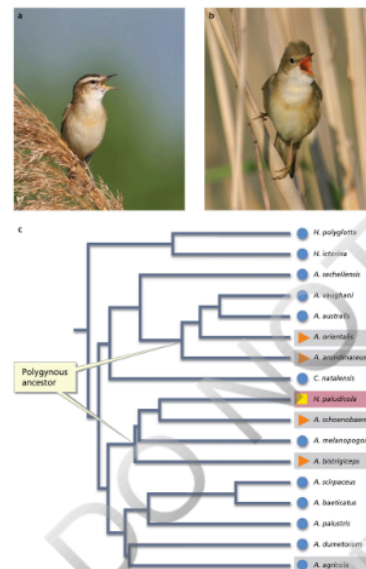
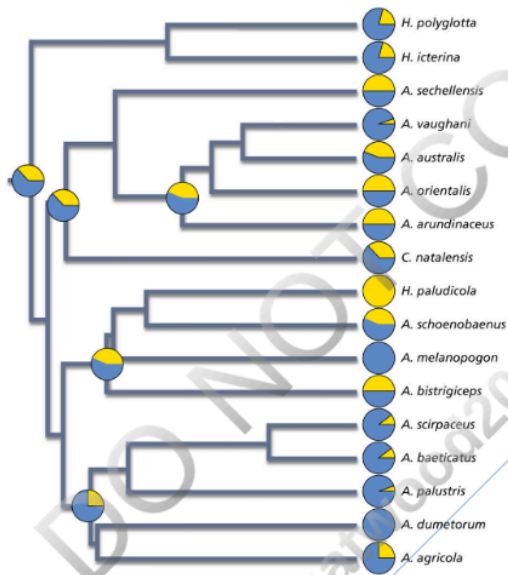


FIGURE 13.6. Reed warbler phylogeny and mating system. (a) *Acrocephalus schoenobaenus* (polygynous). (b) *A. palustris* (monogamous). (c) Phylogeny and mating system. Only four species display polygyny (triangles), indicating that it is probably not the ancestral condition. Because polygyny is found in two separate groups, it appears to have evolved independently at least twice. The majority of species are monogamous (circles), indicating that this system is likely the ancestral condition. The square indicates a single case of promiscuity. Gray: medium habitat; pink: good habitat; all other species breed in poor quality habitats. (Source: Leisler, Winkler, & Wink 2002)

Leisler and his colleagues used published data on food biomass and prey size to estimate habitat quality, categorized as poor (only small prey size), medium (larger prey size), or good (many large prey), for each species. Poor habitats tended to have dense stands of reeds, bushes, or trees that prohibited light penetration. Medium habitats had more light, and good habitats had abundant light and were highly productive, containing many large prey. The researchers then used previously published studies to characterize the relative level of male care as full (equal to that of the female), reduced, or none. Finally, they created a molecular phylogeny using previously published sequences of the cytochrome-b gene.



They found a strong association between habitat quality and mating system across the 17 reed warbler species studied. Monogamy and high levels of male care were predominant in poor-quality habitats, whereas both polygyny and promiscuity and reduced levels of male care were associated with medium- and good-quality habitats. When behavior was mapped onto the phylogeny, two patterns emerged. First, polygyny appears to have evolved independently in this group at least twice. Second, the phylogeny suggests that the ancestral species was monogamous, with a high level of male care (Figure 13.6c; Figure 13.7). Leisler and colleagues' research suggests that in this group of species, male care co-evolved with the mating system and was reduced or absent in habitats of higher quality that contained more abundant resources.



**FIGURE 13.7. Reed warbler phylogeny and paternal care.** High levels of paternal care (large amount of blue in circle) appear to be ancestral, with reduced male care (less blue in circle) having evolved several times. (Source: [Leisler, Winkler, & Wink 2002](#))

This study supports the model of Emlen and Oring, which predicts that habitats with limited resources should favor monogamy and high levels of male care. Shifts by ancestral species to higher-quality habitats are predicted to be associated with reduced levels of male parental care and with the evolution of polygyny and promiscuity, as observed. Leisler, Winkler, and Wink's work represents one approach to understanding the evolution of mating systems. An alternative is to examine the mating systems of individual species in light of the model proposed by Emlen and Oring. Such work often involves experimental manipulations and tests of different predictions for various mating systems. We now examine examples of such studies for each mating system in turn.

approach to understanding the evolution of mating systems. An alternative is to examine the mating systems of individual species in light of the model proposed by Emlen and Oring. Such work often involves experimental manipulations and tests of different predictions for various mating systems. We now examine examples of such studies for each mating system in turn.

## 13.2 Biparental care favors the evolution of monogamy

### Learning Objectives

After reading this section, you should be able to

- explain why the need for biparental care favors the evolution of monogamy and
- describe how the territorial cooperation and mate guarding hypotheses can explain monogamy in a species.

The Emlen and Oring model predicts that monogamy will be observed in situations when biparental care is essential. Monogamy is rare in mammals, an observation consistent with the model, because female lactation—the secretion of highly nutritious milk from mammary glands—alone can provide all the food needed to raise offspring successfully.

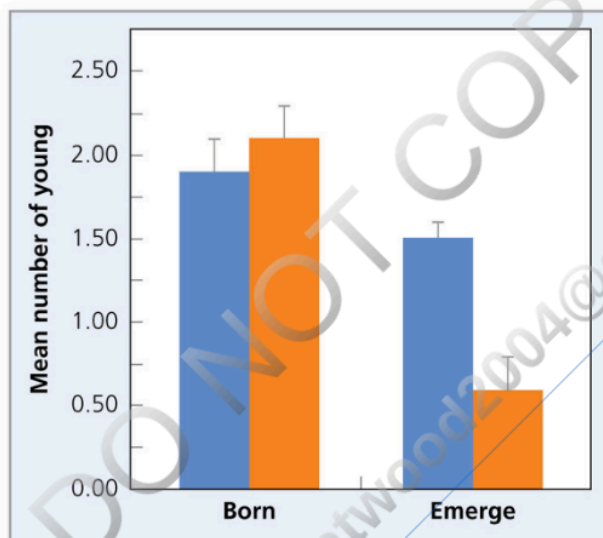
Monogamy does occur in some mammals, including many primates. It is rare, however, in rodents but does occur in the California mouse (*Peromyscus californicus*), which is found throughout California and northern Mexico. Adults form exclusive pair bonds, and genetic data indicate that this species does not mate outside the pair bond ([Ribble 1991](#)). The pair defends a territory, and males assist with all aspects of parental care except lactation. This assistance includes huddling (maintaining close body contact with pups in order to warm them), grooming the young, and carrying them from one location to another ([Gubernick & Alberts 1987](#)). Is male care critical for offspring survival in this species?

### FEATURED RESEARCH California mouse monogamy

David Gubernick and Taye Teferi examined how male parental care affects reproductive success in California mice ([Gubernick & Teferi 2000](#)). They conducted an experiment at the Hastings Natural History Reservation in California. All adults were captured regularly with live traps and uniquely marked with numbered ear tags. Females were checked for reproductive condition (pregnant or lactating) and weighed. The researchers created “male-absent” families by removing a male from a family within three days of the birth of the season's first litter. In the control “male-present” treatment, males were trapped and handled but then released and allowed to return to their families. The researchers estimated the number of young born to each female by comparing her weight

loss between the last days of pregnancy and the time of first capture after giving birth. A standard formula was used to convert body mass loss to offspring number.

There was no difference in the number of offspring born to females that had their male removed and the number of offspring born to those that did not. However, the absence of the father and his parental care significantly reduced offspring survival: significantly more young survived from the male-present families than did from the male-absent families (Figure 13.8). Although males cannot feed offspring, they can assist with thermoregulation and protection. The researchers concluded that the need for biparental care appears to have favored the evolution of monogamy in this species. It is not clear why this rodent is unusual in its requirement for biparental care.



**FIGURE 13.8. Offspring survival.** Mean (+ SE) number of young. Families with fathers (blue) had more offspring survive (i.e., emerge from the nest) than did families without fathers (orange). (Source: Gubernick & Teferi 2000)

## FEATURED RESEARCH Monogamy and biparental care in poison frogs

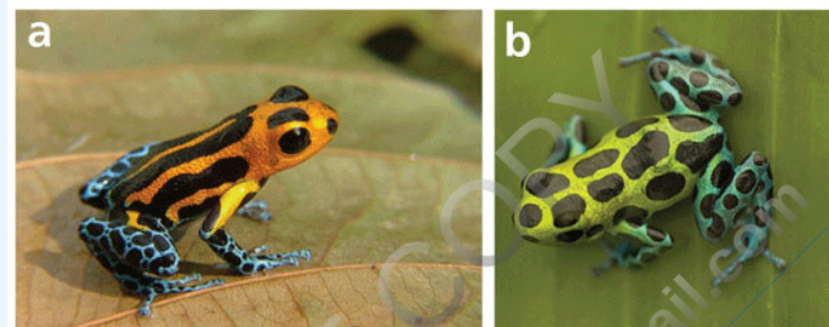
A second example of the role biparental care plays in the evolution of monogamy comes from tropical frogs. Jason Brown, Victor Morales, and Kyle Summers examined the mating systems of two closely related species of poison frogs, *Ranitomeya imitator* and *R. variabilis*, in Peru (Brown, Morales, & Summers 2010) (Scientific Process 13.1). Both species rear their young in a phytotelma, a small pool of water that collects at the base of leaves or petals in a plant. The small size of these pools reduces predation, but it also limits the quantity of nutrients and other resources available for the developing offspring. *R. imitator* rears its tadpoles in very small pools, averaging 24 mL in volume, while *R. variabilis* prefers larger pools, averaging 112 mL in volume.

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pools, averaging 24 mL in volume, while *R. variabilis* prefers larger pools, averaging 112 mL in volume.

### SCIENTIFIC PROCESS 13.1

#### Biparental care and monogamy in poison frogs



**FIGURE 1. Poison frogs with different mating systems.** (a) *R. imitator* is monogamous. (b) *R. variabilis* is promiscuous.

**Research Question:** Why does *R. imitator* have a monogamous mating system, while *R. variabilis* is promiscuous?

#### Hypothesis:

When resources are limited, monogamy will evolve because biparental care is required to successfully raise offspring.

#### Prediction:

Tadpoles in resource-limited small pools will exhibit high survivorship only with biparental care.

#### Methods:

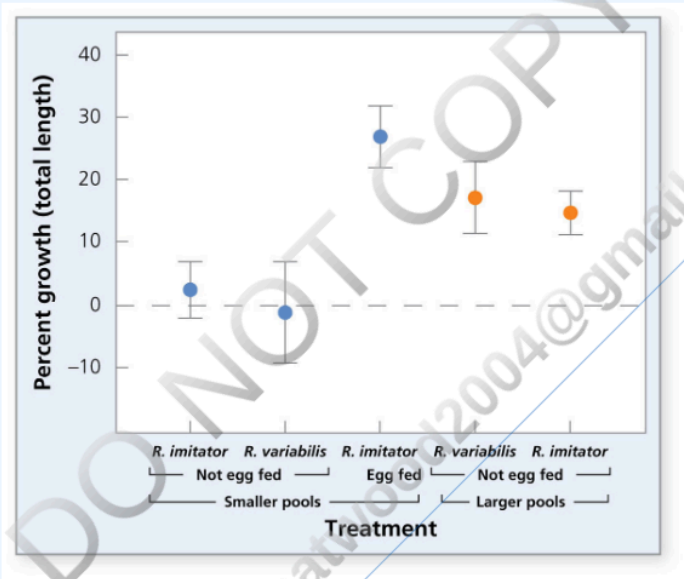
The researchers:

- Manipulated phytotelma pool size. Individual tadpoles of each species were placed in either small (17 mL, on average) or large (39 mL, on average) pools and did not receive female feeding. In the control, *R. imitator* individuals were placed in a small pool and received parental care in the form of female feeding.
- Visited each pool weekly for three weeks to record size (growth rate) and mortality of individuals

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Results:

- For both species, individuals in large pools had high growth rates and high survivorship.
- In small pools with no parental care, individuals of both species had low growth rates and low survivorship.
- *R. imitator* controls in small pools with biparental care had high growth rates and high survivorship.



**FIGURE 2. Growth rate.** Mean ( $\pm$  SE) percent growth. In the small pool treatments (blue), only offspring that were fed exhibited high growth. All offspring in large pools (orange) exhibited high growth rates, even though they were not fed. (Source: [Brown, Morales, & Summers 2010](#))

**Conclusion:**

The need for biparental care in *R. imitator* likely provides strong selection that favors monogamy in this species.

**Evaluate**

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Previous work suggested that *R. imitator* was monogamous with biparental care ([Brown et al. 2008](#)). Females lay from one to three eggs in dense foliage. Males fertilize the eggs, carry each hatchling to a phytotelma for development, and provide protection. Females deposit trophic (unfertilized) eggs in the phytotelma to nourish the young.

**Video: *Ranitomeya imitator* calling in bromeliad phytotelma**

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Video: *Ranitomeya imitator* calling in bromeliad phytotelma

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#### Video: *Ranitomeya imitator* carrying tadpole

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Video: *Ranitomeya imitator* carrying tadpole

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In contrast, *R. variabilis* is promiscuous and raises its young with only male care. Females lay eggs that are fertilized by a male, which then carries the young to a large phytotelma. Males provide parental care, but this care involves only defense, and offspring are not fed by the female (Brown et al. 2008).

Brown and his colleagues examined whether an ecological factor, the size of the breeding pool, is associated with the evolution of parental care. Do larger pools provide enough resources for male-only parental care, whereas smaller pools require biparental care? To examine the importance of parental care for these species, the researchers conducted a transplant experiment. They placed tadpoles of these species into either a large or a small natural phytotelma, with just one species per pool of water. They then placed a mesh screen over the top of the phytotelma to prohibit the addition of resources. None of the experimental tadpoles received parental feeding. In the control, *R. imitator* tadpoles were placed in small pools and did receive parental feeding. The researchers surveyed the pools each week and measured and weighed each tadpole at the start and end of the experiment.

Tadpole growth rate differed significantly across treatments. With no parental care, individuals of both species in large pools had higher growth rates than those in small pools. However, control *R. imitator* tadpoles in small pools that were fed also had high growth rates. The only mortality observed occurred in small pools where the tadpoles received no feeding: four of the eight *R. variabilis* and three of the eight *R. imitator* young in this treatment died during the experiment.

In this species, offspring growth rate strongly affects survivorship, which demonstrates the benefit of biparental care for *R. imitator* offspring raised in a small phytotelma. Because they rear offspring in small pools with limited resources, *R. imitator* adults must provide biparental care and feeding to their offspring in order for these offspring to develop successfully. The researchers concluded that this need has favored the evolution of monogamy, a mating system that is very rare in amphibians. But why don't *R. imitator* lay their eggs in large phytotelmata, where there would be no need for biparental care? One possibility is that *R. imitator* is a poor competitor, and competition for large phytotelmata may be intense. By laying eggs in a small phytotelma, *R. imitator* faces less competition from other species, but doing so requires increased parental investment in the form of biparental care.

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competition from other species, but doing so requires increased parental investment in the form of biparental care.

## FEATURED RESEARCH Monogamy without biparental care in snapping shrimp

The need for biparental care is thought to explain the evolution of monogamy in many species. Yet monogamy does occur in some species that lack biparental care, including coral reef fishes, some mammals, and several species of crustaceans (Mathews 2002). Two hypotheses, which are not mutually exclusive, have been proposed to explain monogamy in such species. The **territorial cooperation hypothesis** states that because two individuals can better defend a critical resource, such as a safe refuge, than can a single individual, selection may favor pair formation and shared defense. The **mate guarding hypothesis** states that selection may favor males that guard females by remaining in close association with them over the course of one or more reproductive cycles. This behavior allows a male to monopolize a single female, but it also prevents both partners from seeking other mates. Both hypotheses make assumptions about the environment. In the first, competition for limited territories is assumed to be intense, or predation outside a safe refuge within the territory is assumed to be high. In the second, a male's encounter rate with females is assumed to be low, perhaps because females are rare or difficult to locate.

Lauren Mathews tested both hypotheses in the snapping shrimp (*Alpheus angulatus*) in a series of studies (Mathews 2002; Mathews 2003). Snapping shrimp are small crustaceans (< 5 cm in length) that live in burrows in intertidal rubble habitats. Most individuals live in male-female pairs within a single burrow (Mathews 2002). However, the female provides all parental care: she broods the eggs on specialized abdominal appendages and then carries, cleans, and aerates them during their development. Both males and females are territorial and will construct and defend a burrow that provides protection from predators. Females are sexually receptive for only a short period of time after molting. Mate guarding by a male can thus enhance his fitness, particularly if he can accurately assess time to molting, as a female close to molting should be of high quality.

Mathews tested a prediction for each hypothesis. The territorial defense hypothesis predicts that pairs of shrimp should defend a burrow more successfully than a solitary individual, while the mate guarding hypothesis predicts that males should tend to guard females that are closer to sexual receptivity (Scientific Process 13.2). Mathews collected shrimp from a site in Florida and housed them in the lab in aquaria. In the territory cooperation experiment, she allowed single females and females paired with a male to guard their burrow from an intruder. She found that females paired with a male were more successful in burrow defense than solitary females. In the mate guarding experiment, she gave males the opportunity to choose and guard a female close to sexual receptivity or one that was not close to sexual receptivity. Females that are about to molt are considered close to sexual receptivity (high-value) and females that have previously molted are not close to sexual receptivity (low-value). She found that males chose to guard high-value females more often than low-value females. This finding suggests that males can assess female condition and modify their territorial defense behavior according to female molting state, in line with the mate guarding hypothesis.

### SCIENTIFIC PROCESS 13.2 Monogamy in snapping shrimp



Research Question: Why are snapping shrimp monogamous?

#### Territorial Cooperation Hypothesis:

Selection favors pair formation for shared resource defense.

#### Prediction:

Pairs of shrimp should defend a burrow more successfully than individuals.

#### Methods:

The researcher:

- Had two treatments: (1) resident female alone and (2) resident female paired with a male.
- Allowed residents to construct burrow for 24 hours.
- Added a single female intruder.
- After 24 hours recorded location of the females. The female in the burrow was the "winner."

#### Results:

- Paired resident females won more burrow contests than single females.

- Paired resident females won more burrow contests than single females.



**FIGURE 1. Burrow defense.** Resident females paired with a male were more likely to be in the burrow after 24 hours (Source: Mathews 2002).

#### Conclusions:

- Females paired with a male were more successful defending a burrow than single females.
- This supports the territorial cooperation hypothesis.

#### Mate Guarding Hypothesis:

Selection favors males that mate with and guard one female.

#### Prediction:

Males should guard females that are closer to sexual receptivity.

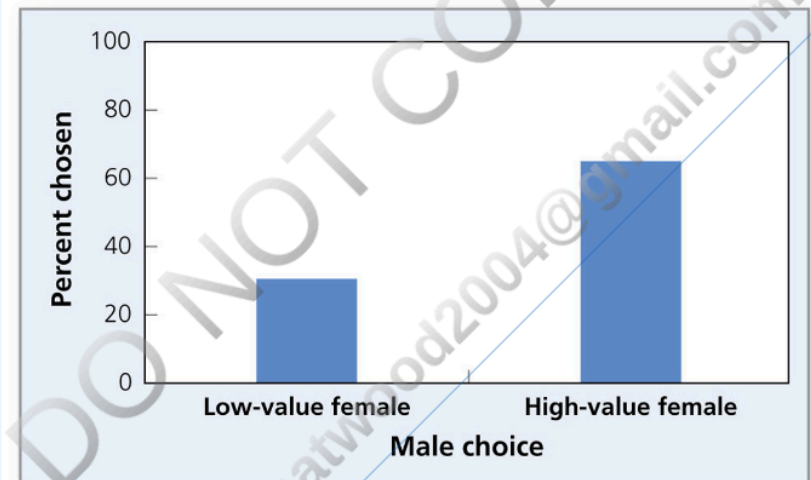
#### Methods:

The researchers:

- Added two females to the test chamber, one female close to sexual receptivity (high-value) and one female far from sexual receptivity (low-value).
- Allowed residents to construct burrows for 24 hours.
- Added a single male.
- After 24 hours recorded the location of the male.

#### Results:

- Males paired with the high-value female more often than the low-value female.



**FIGURE 2. Male choice.** Males paired with high-value females more often than low-value females (Source: Mathews 2003).

#### Conclusions:

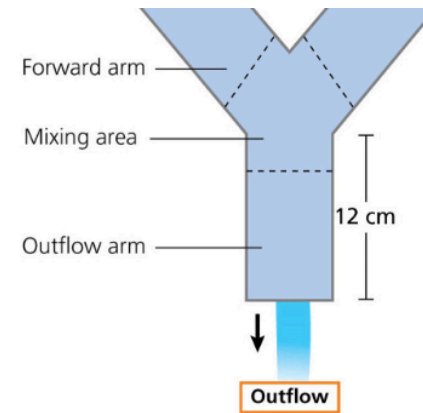
- Males are more likely to pair and guard a high-value female.
- This supports the mate guarding hypothesis.

#### Evaluate



## Evaluate

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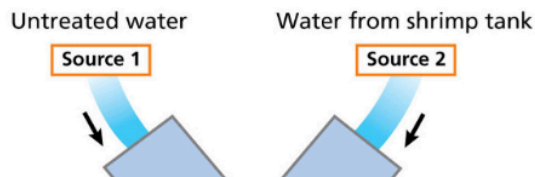


**FIGURE 13.9. Y-shaped maze design.** One source tank contained water that included a shrimp, and the other contained untreated water. A male was placed in the outflow arm and its movement was recorded to determine if it exhibited a preference for one forward arm or the other. Arrows show direction of water flow. (Source: Mathews 2003)

Mathews concluded that both territorial cooperation and mate guarding have favored monogamy in snapping shrimp. Paired individuals, especially females, can more successfully defend territories. Males can assess female condition and thus tend to guard females close to sexual receptivity. Mathews does point out that because of the experimental design, she is not able to rule out the possibility that female behavior or the effect of chemical cues could influence male pairing decisions. More work is needed to investigate these possibilities.

The previous three examples reveal conditions that favor the evolution of monogamy, such as the need for biparental care or two individuals defending a breeding site. Next, we turn our attention to the different forms of polygamy.

Mathews further examined how males are able to determine female sexual receptivity (Mathews 2003). In a new experiment, a water source was attached to each arm of a Y-shaped maze (Figure 13.9). One water source (the treatment) contained a shrimp, and the other did not (untreated water). She used seven different treatments, varying the sex of the shrimp and its molting state. She tested water with pre-molt, inter-molt, and post-molt males and females and a control (untreated water) and recorded the behavior of test males as water flowed through the Y-shaped maze. She found that males only moved toward the pre-molt female water, indicating that they are able to determine, and are attracted to, females close to sexual receptivity.



Mathews tested a prediction for each hypothesis. The territorial defense hypothesis predicts that pairs of shrimp should defend a burrow more successfully than a solitary individual, while the mate guarding hypothesis predicts that males should tend to guard females that are closer to sexual receptivity ([Scientific Process 13.2](#)). Mathews collected shrimp from a site in Florida and housed them in the lab in aquaria. In the territory cooperation experiment, she allowed single females and females paired with a male to guard their burrow from an intruder. She found that females paired with a male were more successful in burrow defense than solitary females. In the mate guarding experiment, she gave males the opportunity to choose and guard a female close to sexual receptivity or one that was not close to sexual receptivity. Females that are about to molt are considered close to sexual receptivity (high-value) and females that have previously molted are not close to sexual receptivity (low-value). She found that males chose to guard high-value females more often than low-value females. This finding suggests that males can assess female condition and modify their territorial defense behavior according to female molting state, in line with the mate guarding hypothesis.

### SCIENTIFIC PROCESS 13.2

#### Monogamy in snapping shrimp



Research Question: Why are snapping shrimp monogamous?

#### Territorial Cooperation Hypothesis:

Selection favors pair formation for shared resource defense.

#### Prediction:

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Pairs of shrimp should defend a burrow more successfully than individuals.

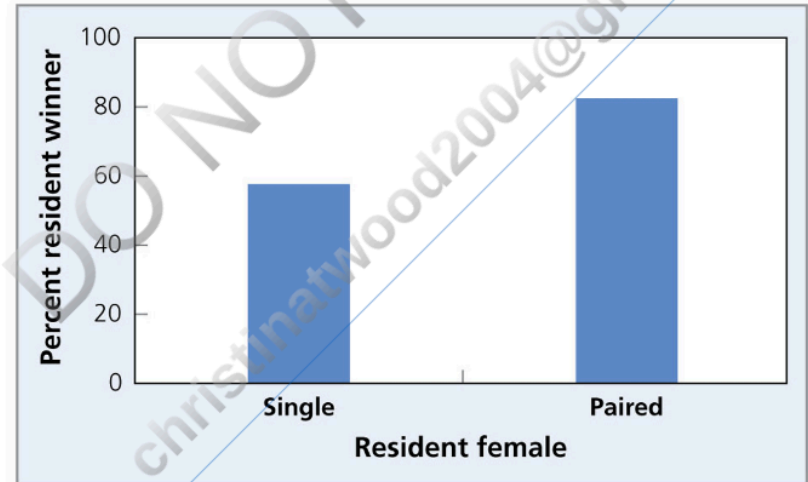
#### Methods:

The researcher:

- Had two treatments: (1) resident female alone and (2) resident female paired with a male.
- Allowed residents to construct burrow for 24 hours.
- Added a single female intruder.
- After 24 hours recorded location of the females. The female in the burrow was the "winner."

#### Results:

- Paired resident females won more burrow contests than single females.



**FIGURE 1. Burrow defense.** Resident females paired with a male were more likely to be in the burrow after 24 hours (Source: [Mathews 2002](#)).

#### Conclusions:

- Females paired with a male were more successful defending a burrow than single females.

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- Females paired with a male were more successful defending a burrow than single females.
- This supports the territorial cooperation hypothesis.

### Mate Guarding Hypothesis:

Selection favors males that mate with and guard one female.

### Prediction:

Males should guard females that are closer to sexual receptivity.

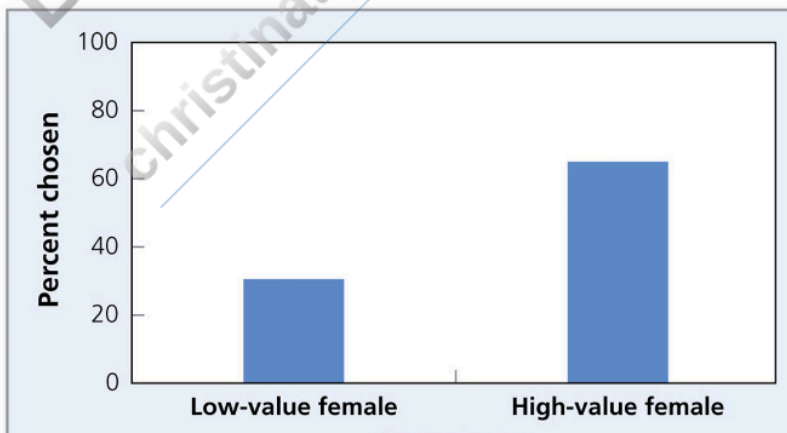
### Methods:

The researchers:

- Added two females to the test chamber, one female close to sexual receptivity (high-value) and one female far from sexual receptivity (low-value).
- Allowed residents to construct burrows for 24 hours.
- Added a single male.
- After 24 hours recorded the location of the male.

### Results:

- Males paired with the high-value female more often than the low-value female.



## Male choice

**FIGURE 2. Male choice.** Males paired with high-value females more often than low-value females (Source: Mathews 2003).

### Conclusions:

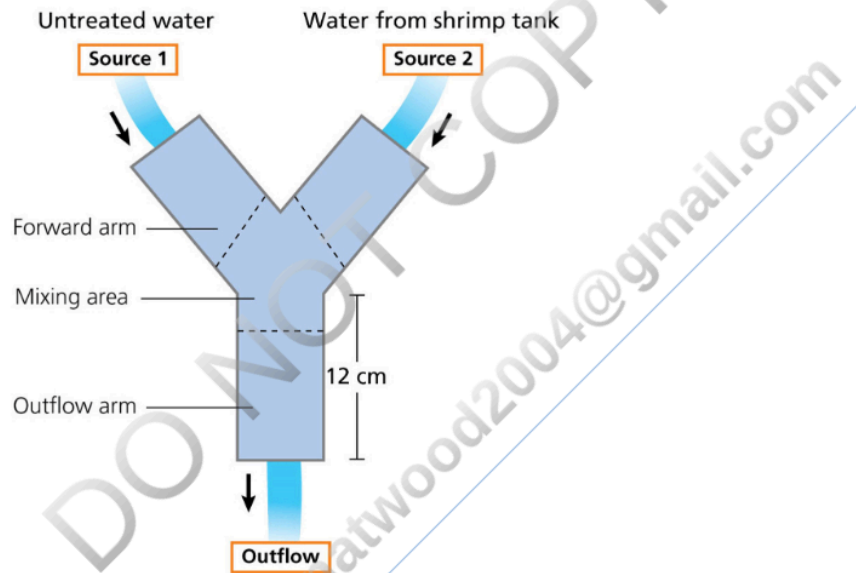
- Males are more likely to pair and guard a high-value female.
- This supports the mate guarding hypothesis.

### Evaluate

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Mathews further examined how males are able to determine female sexual receptivity (Mathews 2003). In a new experiment, a water source was attached to each arm of a Y-shaped maze (Figure 13.9). One water source (the treatment) contained a shrimp, and the other did not (untreated water). She used seven different treatments, varying the sex of the shrimp and its molting state. She tested water with pre-molt, inter-molt, and post-molt males and females and a control (untreated water) and recorded the behavior of test males as water flowed through the Y-shaped maze. She found that males only moved toward the pre-molt female water, indicating that they are able to determine, and are attracted to, females close to sexual receptivity.



**FIGURE 13.9. Y-shaped maze design.** One source tank contained water that included a shrimp, and the other contained untreated water. A male was placed in the outflow arm and its movement was recorded to determine if it exhibited a preference for one forward arm or the other. Arrows show direction of water flow. (Source: Mathews 2003)

Mathews concluded that both territorial cooperation and mate guarding have favored monogamy in snapping shrimp. Paired individuals, especially females, can more successfully defend territories. Males can assess female condition and thus tend to guard females close to sexual receptivity. Mathews does point out that because of the experimental design, she is not able to rule out the possibility that female behavior or the effect of chemical cues could influence male pairing decisions. More work is needed to investigate these possibilities.

The previous three examples reveal conditions that favor the evolution of monogamy, such as the need for biparental care or two individuals defending a breeding site. Next, we turn our attention to the different forms of polygamy.

### 13.3 Polygyny and polyandry evolve when one sex can defend multiple mates or the resources they seek

#### Learning Objectives

After reading this section, you should be able to

- utilize the polygyny threshold model to predict polygyny,
- differentiate resource defense from female defense polygyny,
- compare the evidence for the hotshot and hotspot hypotheses for lek evolution, and
- identify the conditions required for polyandry and sex-role reversal.

Because females tend to invest more in parental care than do males, most examples of polygamy involve polygyny. Much work has centered on determining how males defend and mate with multiple females. According to the Emlen and Oring model, they can do so either directly, by defending these females, or indirectly, by defending resources. Let's see how researchers have distinguished these alternatives.

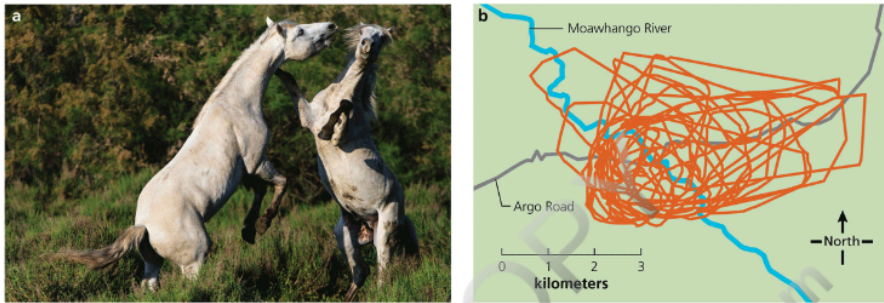
#### FEATURED RESEARCH Female defense polygyny in horses

Feral horses (*Equus caballus*) are found throughout the world in grassland habitats. They live year-round in social units called bands. A typical band consists of one male and up to a dozen adult females. If there are multiple males, a single dominant male obtains most or all of the matings within the band, and so horses exhibit polygyny. Adult males that do not associate with females in bands live in bachelor groups. How can we distinguish between female defense and resource defense polygyny? To do so, we need to determine whether males defend females per se, or whether they simply defend the resources those females use.

Wayne Linklater and his colleagues studied a large population of horses in New Zealand over a three-year period (Linklater et al. 1999; Linklater et al. 2000). Each month, the researchers traveled along regular routes throughout the study site to record the location of bands. Bands were identified by natural markings or by freeze brands previously applied to their coat. The research team plotted the home range of each band using these sightings. In addition, they recorded social behaviors, particularly aggressive interactions between males from different bands.

They found that males aggressively defended their band from other males whenever two bands met or when bachelor males were nearby. During the study, bands overlapped greatly in their home ranges (Figure 13.10). In fact, all bands essentially used the same area, although at different times, and there was no indication of exclusive

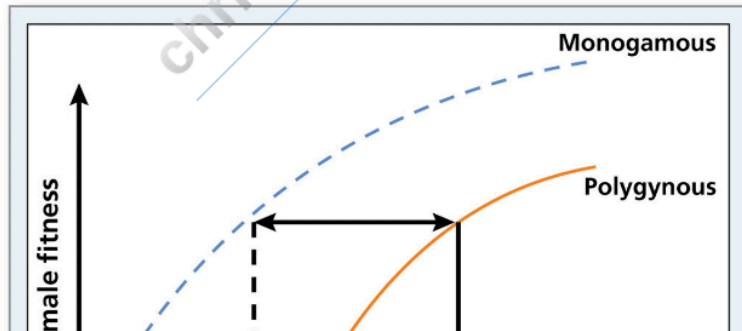
defense of territories, perhaps because territory defense is too costly. This finding suggests that males actively defend females and not resources. In other words, they display female defense polygyny.



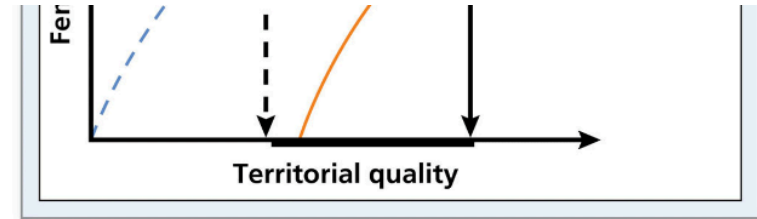
**FIGURE 13.10. Horse bands.** (a) Feral horse aggressive interaction. (b) Bands use similar areas. Here, the areas used by 28 bands are plotted as separate polygons, which overlap greatly. (Source: Linklater et al. 2000)

## FEATURED RESEARCH Resource defense polygyny in blackbirds

In horses, males defend aggregations of females directly. In other species, males defend an area of resources used by females and so can mate with multiple females. If access to resources affects female reproductive success, the **polygyny threshold model** (Verner 1964; Verner & Wilson 1966; Orians 1969) predicts that females should mate polygynously only when the benefits of doing so—access to greater resources—outweigh the cost of sharing resources with other females. Of course, males differ in their ability to defend resources. Some will defend territories rich enough in resources to meet the requirements of multiple females. Others will only be able to defend territories with lower levels of resources—enough, for example, to fulfill the requirements of just a single female. This variability means that females can mate monogamously on a resource-poor territory or can mate polygynously on a resource-rich territory. Females should select the option that leads to higher fitness (Figure 13.11). The model predicts that only males defending resource-rich territories will mate polygynously.



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**FIGURE 13.11. Polygyny threshold model.** The fitness of a female is plotted as a function of territory quality for two options: mating monogamously (dashed blue line) or mating polygynously (solid orange line). To benefit by mating polygynously, territory quality must be substantially higher (represented by the thick line on the x axis).

Stanislav Pribil and William Searcy tested the polygyny threshold model using red-winged blackbirds (*Agelaius phoeniceus*), a species known to mate both monogamously and polygynously. Males defend territories in dense vegetation around lakes and ponds. The researchers tested the model by giving females a choice of mating monogamously in a low-quality territory or polygynously in a territory of higher quality (Pribil & Searcy 2001). In this species, territory quality correlates with nest placement: nests in vegetation over water experience less predation and so are of higher quality than those on land.

### Video: Redwing blackbird pair with nest and chicks over water

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The experiment was conducted at three marshes in Ontario, Canada. At each marsh, when male blackbirds migrated back to breeding sites and started defending territories, the researchers identified similar adjacent territories, or territory dyads. When the first females arrived to settle on territories, one territory in each dyad was randomly chosen to be high quality, and the other was chosen to be low quality. Territory quality was manipulated by adding nesting platforms with cattail (*Typha latifolia*) shoots, which created nesting sites for the blackbirds. In the high-quality territory, the platforms were placed over open water, whereas in the low-quality territory, they were placed on land. All females in the low-quality territory were removed, but one female was allowed to remain in the high-quality territory. This setup created mating options on adjacent territories for newly arriving females. Because the high-quality territory already contained both a resident male and a female, any newly arriving female would mate polygynously if she settled there. In contrast, the low-quality territory contained only a resident male, which ensured that an arriving female would mate monogamously if she chose to settle there. Twice each day, the experimenters recorded the presence of newly settled, nesting females (Figure 13.12).



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with each male receiving eggs from only one female (Berglund, Rosenqvist, & Svensson 1989; Jones, Walker, & Avise 2001). And, while many polyandrous birds live in resource-rich environments, they appear to have evolved from species that lived in resource-poor habitats (Andersson 1995). Thus, the ancestral habitat probably favored male-biased care, but the current habitat allows high female fecundity because there is abundant energy for egg production.

The previous examples illustrate how sex-biased parental care and resource distribution can favor the evolution of polygyny and polyandry, both of which involve multiple mating by just one sex. Next, we examine mating systems that involve multiple matings by both sexes.

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### 13.4 The presence of social associations distinguishes polygynandry from promiscuity

#### Learning Objectives

After reading this section, you should be able to

- distinguish between polygynandry and promiscuity and
- identify the conditions required for scramble competition.

Polygynandry and promiscuity differ based on the existence of social associations: mating occurs within specific groups in a polygynandrous mating system but is not restricted to occur within specific groups in a promiscuous mating system. Emlen and Oring suggest that polygynandry, or plural breeding, will evolve when group defense of a territory is more effective than defense by a single individual. In these cases, a breeding group will consist of several males and females that together defend a large territory and so associate closely with one another. Plural breeding occurs in social carnivores such as African lions (*Panthero leo*), banded mongooses (*Mungos mungo*), and spotted hyenas (*Crocota crocuta*) (Figure 13.20), as well as in several species of primates, including chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*).



FIGURE 13.20. Plural breeding. The spotted hyena (*Crocota crocuta*) exhibits plural breeding.

Such groups are often challenged by rival groups, and large groups are typically more successful than smaller ones in a conflict over a territory. For example, encounters and territorial challenges often occur between lion prides, resulting in intense chases. The larger pride wins over 80% of such interactions (Packer, Scheel, & Pusey 1990), demonstrating the advantage of group defense. In many plural breeding species, the number of males in a social group correlates positively with the number of females, because higher male numbers are required to defend all females successfully as group size increases (Clutton-Brock 1989). The males are often related, and more than one sires offspring (e.g., Cant 2000; Engh et al. 2002).

#### FEATURED RESEARCH Polygynandry in European badgers

One striking example of plural breeding is found in the European badger (*Meles meles*) (Figure 13.21). This large carnivore ranges throughout Europe and Asia and exhibits much variation in sociality. In Great Britain, badgers live in social groups of up to two dozen individuals. Such groups contain multiple reproductively active males and females, suggesting the possibility of polygynandry.





**FIGURE 13.21. European badgers.** A species that lives in social groups in Great Britain and exhibits a plural mating system.

Hannah Dugdale and her colleagues investigated the mating system of a population of badgers in Wytham Woods, Oxford, England (Dugdale et al. 2007). Over a period of 17 years, adults and cubs from different social groups were captured and uniquely marked with a tattoo. The researchers took blood samples for DNA extraction to determine the parentage of over 300 cubs. By determining the parentage of the cubs, they could also determine which adults were breeding in each group.

#### Video: Badger research at Wytham Woods

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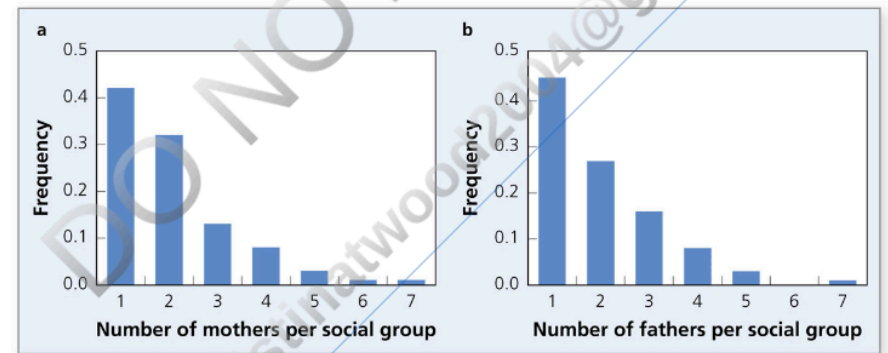
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On average, social groups contained 12 adults, six of each sex, and approximately 27% of all adult males and 31% of adult females bred successfully each year. Within social groups, an average of 1.6 females per group gave birth each year and 1.5 males sired offspring, but as many as five males and five females reproduced in a social group (Figure 13.22). Because multiple males and females reproduced within social groups, these data provide clear evidence of a plural breeding system. Why do multiple males, rather than just one, mate with many females? Mating occurs year-round in England, which reduces the likelihood of male mate guarding, because such a behavior would likely be too costly for a single male attempting to successfully guard all the females (Yamaguchi, Dugdale, & MacDonald 2006). In addition, females could benefit by mating with multiple males to ensure fertilization, reduce harassment from males, or increase the genetic diversity of their offspring, as we will see later. Males from outside a group do sire offspring in some groups (Annavi et al. 2014), and perhaps multiple males can better defend a group of females from such outsiders than can a single male. Further work is required to better understand the fitness benefits that such a mating system provides to males and females.



**FIGURE 13.22. Badger reproduction.** The frequency of social groups with different numbers of adult (a) females and (b) males that reproduced within the group. In most groups, multiple males and females produced offspring. (Source: Dugdale et al. 2007)

## FEATURED RESEARCH Promiscuity and scramble competition in seaweed flies and red squirrels

Emlen and Oring suggest that promiscuity will evolve when the costs of the defense of mates or resources exceed the benefits and when there is no need for biparental care. In a promiscuous mating system, individual males and females mate with multiple partners in the absence of social associations. There is either uniparental care,

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typically provided by the female, or no parental care.

Promiscuous mating is characterized by **scramble competition**, as individuals compete indirectly with each other to find and secure copulations with multiple mates. This system occurs in many invertebrates. For example, seaweed flies (*Coelopa frigida*) live and breed in decaying seaweed on beaches. They engage in no courtship behavior, and males attempt to copulate with females as soon as they encounter them. A recent study estimated that in one high-density population on St. Mary's Island in England, males mount a female every eight minutes during the day, and a female may mate with hundreds of males during her three-week life span (Blyth & Gilburn 2006).

A less extreme example of promiscuity is found in red squirrels (*Tamiasciurus hudsonicus*). These North American diurnal rodents live in coniferous forests, and males and females defend separate, permanent territories. Jeffrey Lane and colleagues studied the mating system of a population of red squirrels near Kluane National Park in southwest Yukon, Canada (Lane et al. 2008). They captured and marked individuals with numbered ear tags and collected tissue samples for DNA analysis. Each ear tag also contained two uniquely colored wires that facilitated identification from a distance. Females were fitted with radio transmitters and monitored daily to assess reproductive behavior.

In red squirrels, females are receptive for a single day, when they relax territorial defense; on these days, multiple males visit their territory, often simultaneously, and engage in "mating chases." Some chases result in copulations (Figure 13.23). On these days, the researchers followed the female for an average of 9.5 hours and recorded all chases and copulations. After females gave birth, researchers visited each nest and collected tissue samples from all offspring for DNA analysis to determine paternity.



**FIGURE 13.23. Red squirrels.** Each individual red squirrel defends a separate territory from others. Here, two marked individuals mate.

Females copulated with an average of 5.8 males. For females that raised more than one young, 82.5% of litters were sired by multiple males, with a mean of 2.3 sires per litter. These data demonstrate that the mating system of the red squirrel is promiscuity with scramble competition for mates. Multiple males search for receptive females and then attempt to mate with them. Many males are successful, and so both males and females mate with multiple partners.

In this system, males and females each have large territories. It is unlikely that a single male could successfully defend a territory of twice-normal size so as to secure sufficient food for himself and his mate. In addition, a female's ability to move about freely and her running behavior make economical defense of her unlikely. These two factors therefore favor the evolution of promiscuity in this species. You may be wondering why females mate with multiple males. What benefit do females obtain from this behavior? We address this important question next.



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### 13.5 Social and genetic mating systems differ when extra-pair mating occurs

#### Learning Objectives

After reading this section, you should be able to

- differentiate social from genetic mating systems,
- outline the factors that can explain the evolution of multi-male mating by females, and
- describe how the genetic quality hypothesis can explain the benefits of extra-pair matings.

Mating system classifications were originally developed from observations of individuals and their pair-bond associations, under the assumption that individuals only mated with their social partner(s); these classifications are known as **social mating systems**. With the advent of DNA fingerprinting techniques (Toolbox 13.1), we have learned that social mating systems often differ from **genetic mating systems**, which describe the actual number of sexual partners that contribute to a set of offspring, because both males and females mate outside of existing pair bonds and social associations. For instance, roughly 90% of socially monogamous bird species engage in **extra-pair copulations (EPCs)**, which result in extra-pair offspring (Griffith, Owens, & Thuman 2002). Such behavior is widespread across taxa (e.g., Sefc et al. 2008; Cohan & Allainé 2009). Together, these observations have led to the description of extra-pair mating systems, which occur when social and genetic mating systems differ because

of extra-pair paternity (e.g., [Stutchbury & Morton 1995](#)). Why are these social and genetic mating systems so different?

To understand the evolution of extra-pair mating, consider a socially monogamous, pair-bonded species. From an evolutionary perspective, it is easy to understand why males seek sexual partners outside the pair bond: doing so can increase their reproductive success. The risk to a male of seeking extra-pair partners is that other males are behaving similarly, so while he is away from his partner, he may lose paternity to other males. On the other hand, a female that seeks extra-pair partners may risk losing parental care from her mate if his paternity is not certain. In general, females cannot increase the number of offspring they produce by mating with multiple males. Given the potential cost and apparent lack of benefits, why do socially monogamous females mate with multiple partners?

Several factors can explain the evolution of multi-male mating by socially monogamous females. In some cases, female fertility can be enhanced ([Pryke et al. 2010](#)) and females can also gain additional protection from predators ([Rodríguez-Muñoz, Bretman, & Tregenza 2011](#)). In addition, female offspring can acquire additional resources if each sexual partner provides some parental care (e.g., [Blomqvist et al. 2005](#)). Furthermore, in some social mammals with multiple males in the group, dominant males may kill unrelated offspring (infanticide). However, if a female mates with multiple males—especially dominant ones—she may be able to protect her offspring from infanticide because paternity will be uncertain and a male will not kill offspring of a female he has inseminated ([Wolff & MacDonald 2004](#); [Lukas & Huchard 2014](#)). However, the most general explanation for multi-male mating is that females can increase the genetic quality of their offspring ([Jennions and Petrie 2000](#)).

## CHAPTER SUMMARY AND BEYOND

Males and females mate with different numbers of partners, and their mating systems range from a single mate (monogamy) to multiple mates for one or both sexes (polygamy). Two factors help explain the evolution of mating systems. First, males and females experience different fitness benefits and costs of parental care. Second, environmental conditions affect the ability of individuals to monopolize, through successful defense, either resources or mates.

Recent work on the evolution of mating systems has focused on selective factors that favor the evolution of genetic monogamy ([Kvarnemo 2018](#)), as well as neuroanatomical and transcriptomic differences among monogamous and non-monogamous pairs of species ([Johnson & Young 2015](#); [Chappell et al. 2016](#); [Renn et al. 2018](#); [Young et al. 2019](#)). Other work focuses on distinguishing resource defense from female defense polygyny (e.g., [Seki et al. 2009](#)) and the role kin selection plays in the evolution of leks ([Reynolds et al. 2009](#)). In many species, the social mating system differs from the genetic mating system, because individuals mate outside of existing pair bonds. Males can increase their fitness by mating with multiple partners, because the number of sexual partners often limits their reproductive fitness. In contrast, female reproductive success is rarely limited by the number of sexual partners, but females can gain additional care or protection for their offspring by mating with multiple males and can acquire genetic benefits for their offspring ([Slatyer et al. 2012](#); [Pizzari & Wedell 2013](#)).

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## CHAPTER SUMMARY AND BEYOND

Males and females mate with different numbers of partners, and their mating systems range from a single mate (monogamy) to multiple mates for one or both sexes (polygamy). Two factors help explain the evolution of mating systems. First, males and females experience different fitness benefits and costs of parental care. Second, environmental conditions affect the ability of individuals to monopolize, through successful defense, either resources or mates.

Recent work on the evolution of mating systems has focused on selective factors that favor the evolution of genetic monogamy ([Kvarnemo 2018](#)), as well as neuroanatomical and transcriptomic differences among monogamous and non-monogamous pairs of species ([Johnson & Young 2015](#); [Chappell et al. 2016](#); [Renn et al. 2018](#); [Young et al. 2019](#)). Other work focuses on distinguishing resource defense from female defense polygyny (e.g., [Seki et al. 2009](#)) and the role kin selection plays in the evolution of leks ([Reynolds et al. 2009](#)). In many species, the social mating system differs from the genetic mating system, because individuals mate outside of existing pair bonds. Males can increase their fitness by mating with multiple partners, because the number of sexual partners often limits their reproductive fitness. In contrast, female reproductive success is rarely limited by the number of sexual partners, but females can gain additional care or protection for their offspring by mating with multiple males and can acquire genetic benefits for their offspring ([Slatyer et al. 2012](#); [Pizzari & Wedell 2013](#)).

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## CHAPTER 12

# Mating Behavior

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### Concepts

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Our yard in the Midwest is quiet all winter long—but each spring, this situation changes dramatically. The first sign of spring is the sound of birds singing each morning. As it gets still warmer, we hear field crickets, and then hundreds of male tree frogs calling in a loud chorus on warm, humid evenings. Why the change? Sex. The silence of winter gives way to the sounds of animals attracting mates.

Some years are especially noisy. Every 13 or 17 years, a brood of periodical cicadas emerge from underground, where they have been feeding on the roots of plants, to mate. Cicadas are hemipterans (true bugs), and North

America is home to seven periodical species. In 2011, two 13-year species emerged (*Magicicada tredecim* and *M.*

*neotredecim*), and our region became awash with cicadas (Figure 12.1). Millions of males were calling females each day. It was so loud that we couldn't spend much time outside, because the sound level frequently exceeded 90 decibels—the equivalent of a jackhammer.



**FIGURE 12.1. Cicadas mating.** Periodical cicada species emerge at high densities only in certain years and males produce a very loud chorus to attract females for mating.

In this chapter, we start by examining how sexual selection can result in dramatic phenotypic differences between males and females by acting on traits that affect reproduction. We then see why females are often more choosy than males when selecting a mate and discuss the numerous benefits associated with selective mating. Female mate choice typically occurs prior to copulation, but we'll see that it can also occur after mating. When females are choosy, selection can favor the evolution of multiple male mating tactics when males cannot successfully compete for mates. Finally, we'll see how mating preferences can be affected by the mating behavior of others.

### Video: Periodic cicada invasion

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## 12.1 Sexual selection favors characteristics that enhance reproductive success

### Learning Objectives

After reading this section, you should be able to

- distinguish mate competition from mate choice,

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- use the Parker model to explain the evolution of anisogamy,
- distinguish between Bateman's hypothesis and Triver's parental investment theory,
- differentiate between traits that are ornaments and those that are weapons, and
- describe how the sensory bias hypothesis can explain the evolution of sexually selected traits.

As we saw in [Chapter 3](#), Charles Darwin proposed natural selection as a mechanism to explain the evolution of adaptive traits in species ([Darwin 1859](#)). Darwin was a devoted naturalist and made copious notes on the morphological differences between male and female genitalia (organs of reproduction), or the **primary sexual characteristics**, in many different species (such traits are often used by researchers to distinguish different species of invertebrates). He also noted many other differences between males and females in traits not directly involved in reproduction, called **secondary sexual characteristics**. For example, in many birds, males have colorful plumage, while females are drab ([Figure 12.2](#)). Many male mammals and insects possess large antlers, horns, or horn-like projections that are not present in females. Darwin observed that such elaborate and exaggerated traits, in conjunction with complex behavioral displays and vocalizations, are often involved in conspecific interactions during the mating season.



**FIGURE 12.2. Exaggerated male traits.** (a) Male northern cardinals (*Cardinalis cardinalis*) possess bright red and black plumage that is absent in (b) females. (c) Male stag beetles (*Lucanus cervus*) possess large horn-like projections that females of that species do not.

Secondary sexual traits puzzled Darwin because they did not seem to fit into his theory of natural selection. Exaggerated morphological and behavioral traits should be energetically expensive to produce and maintain, and they can make individuals more obvious to predators and so reduce their survivorship. How could a male peacock's tail increase its survival? And if it did, why was the exaggerated trait found only in males? In *On the Origin of Species*, Darwin first proposed that exaggerated male traits might be advantageous for reproduction rather than for survival. In a subsequent book, *The Descent of Man and Selection in Relation to Sex*, Darwin in fact hypothesized that these traits might arise from a different form of selection ([Darwin 1871](#)). Sexual selection represents "the advantage certain individuals have over others of the same sex and species solely in respect of reproduction" ([Darwin 1871](#), p. 210). As such, sexual selection is a subset of natural selection.

How does sexual selection explain the evolution of exaggerated male traits? First, Darwin proposed, in many species there is intense competition within one sex (often males) for mating opportunities with the other sex (often females).

For example, males may engage in direct physical combat in which only the winners mate with females. Today, we describe this process as **mate competition (or intrasexual selection)**—when members of one sex compete with one another for mating opportunities ([Figure 12.3](#)). Such competition can include direct aggressive interactions, as well as contests over resources or breeding territories, as we saw in [Chapter 11](#). While such competition is an important aspect of sexual selection, Darwin recognized another aspect as well: females may be choosy. He thus proposed that males may also compete among themselves to increase their attractiveness to females. In this way, he envisioned that females often play an active role in reproductive decisions through **mate choice (or intersexual selection)**—when members of one sex exhibit distinct mating preferences. As we will see, both forms of selection can, and do, occur within a species, often in a sequential manner. Together, mate competition and mate choice create sexual selection, a process that favors characteristics in one sex that allow the trait bearers to be more successful reproductively. Sexual selection is one of the most active areas in animal behavior research today.



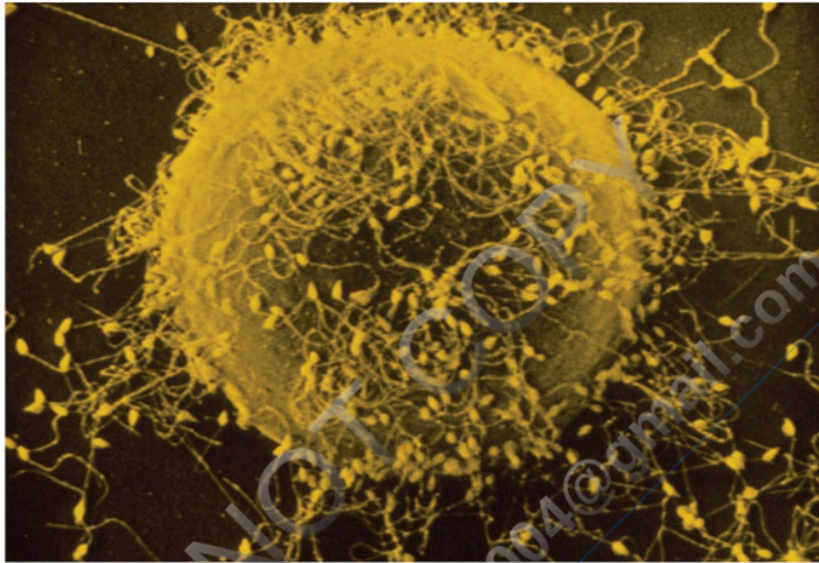
**FIGURE 12.3. Mate competition.** Male northern elephant seals (*Mirounga angustirostris*) compete for females.

## Why two sexes?

Obviously, we could not have sexual selection without two sexes, but how did the two sexes evolve? One fundamental difference between males and females is the size of their gametes ([Figure 12.4](#)). Males tend to produce many small, motile gametes (sperm), while females tend to produce much larger, nutrient-rich, and nonmotile gametes (eggs), a phenomenon called **anisogamy**. In many algae, fungi, and unicellular protozoans,



however, all individuals produce similar-sized gametes; this **isogamy** appears to be the ancestral form (Bell 1978; Bulmer & Parker 2002). How did anisogamy evolve from isogamy?



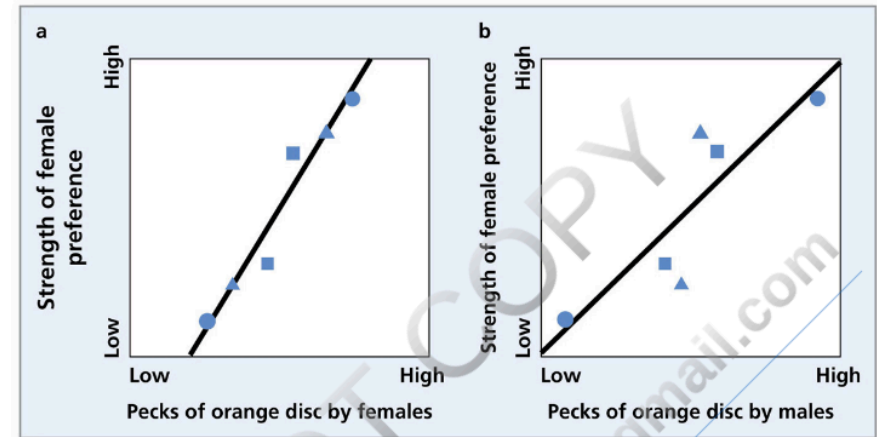
**FIGURE 12.4. Gametes.** A single sea urchin egg cell surrounded by hundreds of sperm cells.

Geoff Parker and colleagues developed a model to answer this question (Parker, Baker, & Smith 1972; Bulmer & Parker 2002). This model is based on the following assumptions:

1. In the ancestral marine environment, individuals in a population that retain reproductive compatibility produce different-sized gametes.
2. Each parent has a fixed amount of energy to allocate to gamete production, resulting in a size–number trade-off: as the number of gametes produced increases, their size will decrease.
3. Zygote viability is related to its size. Larger zygotes have higher viability because they contain more resources for survival.

Parker considered the fitness of individuals that produce only small, large, or intermediate-sized gametes. Small gametes have a numerical advantage: they will

strongest female preference for orange males, both sexes displayed the strongest attraction to the orange discs (Figure 12.12).



**FIGURE 12.12. Mating and food color preferences.** In populations where females most strongly preferred orange males (y axis), both (a) females and (b) males pecked the orange-colored disc most frequently. Each symbol represents a different population. (Source: Rodd et al. 2002)

These experiments indicate that both male and female guppies display an innate preference for orange objects. This finding provides support for the hypothesis that female mating preference could be linked to a preexisting preference for orange food objects. In Section 12.3, we'll examine additional hypotheses to explain female trait preferences.

In all these cases, we see that sexual selection can explain the evolution of certain traits because they enhance reproductive success. For traits used in mate competition, the selective advantage is easy to see: larger weapons can provide an advantage in direct competition with rivals. Furthermore, it is straightforward to understand how a trait favored by one sex in their choice of a mate will evolve in the other sex, because those that possess the most extreme form of the trait will have high reproductive success.

Less clear, however, are the benefits of mate choice. At the beginning of the chapter we noted that in most species, females are often the choosy sex. What benefits can females gain by such choosiness? We examine that question next.

## 12.2 Females select males to obtain direct material benefits

## Learning Objectives

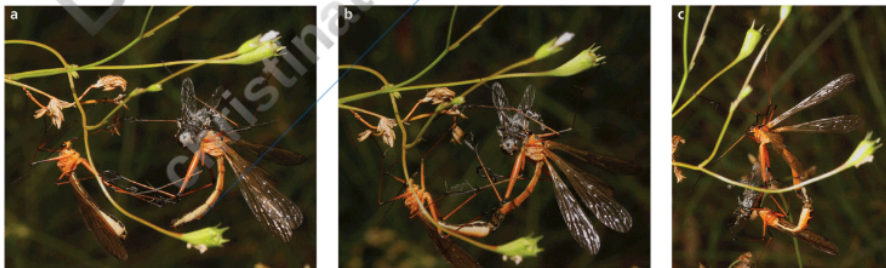
After reading this section, you should be able to

- provide examples of direct material benefits females can obtain through mate choice and
- explain the potential fitness benefits from mate choice.

Parental investment theory predicts that the sex that invests the most time and energy in offspring can benefit by being selective in its choice of mates. As we saw, this usually means that females are choosy. What are the benefits of being selective? Two possibilities exist (Andersson & Simmons 2006). First, females can benefit by choosing males that provide **direct material benefits**, such as food gifts, access to territories with abundant food, or enhanced parental care (Møller & Jennions 2001). Second, females can benefit by mating with males that provide **indirect genetic benefits** that enhance the fitness of offspring. In this section, we examine how females can benefit directly from selective mate choice.

## FEATURED RESEARCH Female choice and nuptial gifts in butterflies

In many arthropods, males provide a **nuptial gift** to a female prior to or during mating that provides nutrition and so can increase her reproductive success (Figure 12.13). These gifts can be prey, carrion, plant material, or glandular secretions (Vahed 2007). In some species, females prefer to mate with larger males because they offer large nuptial gifts (Gwynne 1982).



**FIGURE 12.13. Nuptial gift.** (a) A male hanging fly (*Bittacus* sp.) (right) presents a nuptial gift (dead fly) to a female (left). (b) The pair copulates. (c) The female takes the gift to eat.

Nina Wedell and Bengt Karlsson studied whether nuptial gifts enhance female reproductive success in butterflies (Wedell & Karlsson 2003). Male green-veined white butterflies (*Pieris napi*) (Figure 12.14) provide a

spermatophore—sperm packaged within a protein-rich structure produced by male accessory glands—as a nuptial gift. Once inside a female, the spermatophore disintegrates, releasing its nutrients, which the females can allocate to reproduction. Because adults feed mainly on nectar, the spermatophore can represent an important protein source. Does it affect female fitness?

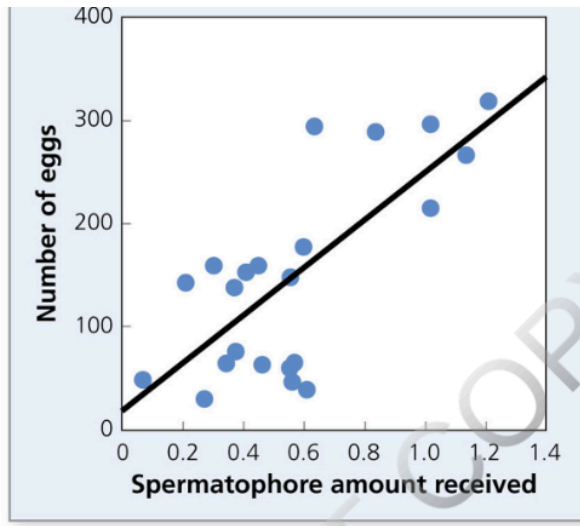


**FIGURE 12.14. Green-veined white butterflies mating.** The male spermatophore provides nutrients to the female.

Wedell and Karlsson examined whether a female's egg production, a surrogate of her fitness, varied positively with the size of the nuptial gift received from a male. To do so, they needed to quantify how much resource transferred from the male became incorporated into egg production. They did this by feeding males radioactively labeled leaves containing either  $^{14}\text{C}$  or  $^3\text{H}$ , which then became incorporated into his spermatophore. They then calculated the rate that the spermatophore disintegrated in the female's abdomen to calculate the amount of spermatophore the female received.

The researchers allowed a female to mate with a single male and lay eggs, which were then collected and dried. Each female was sacrificed to obtain her thorax and abdomen for analysis. The female's eggs, abdomen, and thorax were tested for radioactivity to quantify the amount of male nutrients transferred from the male to the female in the spermatophore. Females receiving more resources from the male (larger spermatophores) produced more eggs (Figure 12.15), showing a direct benefit of male nuptial gift on female fecundity. Females can benefit directly by mating with males that offer large nuptial gifts.

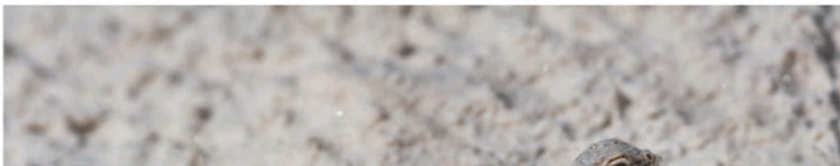




**FIGURE 12.15. Nuptial gift and egg production.** Number of eggs laid by females in relation to the amount of spermatophore nutrients received from males. (Source: [Wedell & Karlsson 2003](#))

## FEATURED RESEARCH Female choice and territory quality in lizards

Another direct benefit of mate choice for females is access to high-quality resources defended by a territorial male. Ryan Calsbeek and Barry Sinervo examined how territory quality affects female choice and fitness in side-blotched lizards (*Uta stansburiana*) ([Figure 12.16](#)) ([Calsbeek & Sinervo 2002](#)). Males defend territories where they display to females from rock perches. The quality of a territory is based on its rockiness: rocks provide perches not only to display to females but also to spot predators. Rocks also increase the range of “microclimates” (both hot and cool locations) available for thermoregulation, an important physiological factor for ectotherms like lizards. Previous work demonstrated that offspring growth and survival are greater when females lay eggs within male territories that have many rocks ([Calsbeek et al. 2002](#)). In this system, males compete for territories with abundant rocks, and females prefer to mate with males that control the rockiest territories—that is, the best males defend high-quality territories. However, that preference makes it difficult to know whether female mate choice is based on male quality or the quality of his territory.



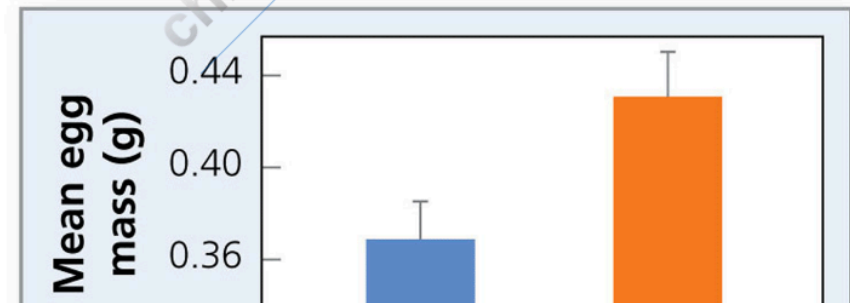
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**FIGURE 12.16. Side-blotched lizard.** Males defend territories to attract females.

To find out, the researchers manipulated territory quality after males had established their territories but before females became receptive and selected mates. They first mapped male territories and observed that large, dominant males settled on those territories with the most rocks. Then the researchers moved ten to 40 rocks from the territories of large, dominant males to the territories of small neighboring males. The added rock piles increased territory quality for small males while reducing territory quality for large males, because all males remained on their original territory after the manipulation. This design allowed the researchers to successfully separate high-quality males from high-quality territories. At the end of the breeding season, after females had selected mates, females were captured and brought into the laboratory to lay their eggs, which were incubated under standard conditions. The researchers measured the egg-laying date and egg mass of each female.

They found that females strongly preferred the improved territories, even though they were occupied by small males. Of the 51 females in the population, 37 settled on the improved plots. Females on improved territories laid eggs sooner and produced larger egg masses ([Figure 12.17](#)), demonstrating a direct fitness benefit for females that select high-quality territories. In this system, females appear to select mating partners based on male territory quality and derive a significant fitness benefit from doing so.



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**FIGURE 12.17. Female egg mass.** Mean (+ SE) egg mass of females on treatment territories. Females on improved territories produced larger egg masses. (Source: [Calsbeek & Sinervo 2002](#))

We have seen that females can benefit by selecting males that provide access to a material benefit: resources. In many species, however, males do not provide material benefits, and still females are selective in their choice of a mate. Why? This is where indirect benefits enter the equation, as we are about to see.

#### Featured Research Female choice and territory quality in lizards

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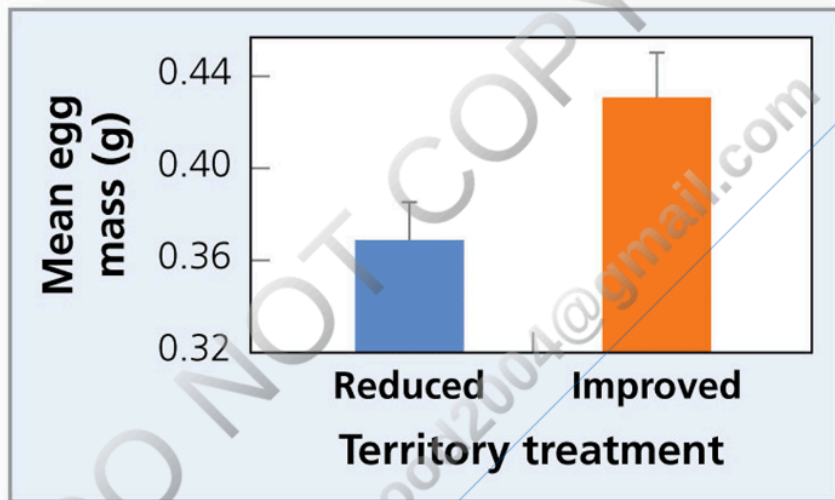


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### 12.3 Female mate choice can evolve via indirect benefits to offspring

#### Learning Objectives

After reading this section, you should be able to

- provide examples of indirect material benefits females can obtain through mate choice,
- differentiate between Fisher's runaway process of sexual selection, mate choice for good genes, and the handicap principle, and
- describe the Hamilton-Zuk hypothesis.

In many species, females benefit not from direct material benefits, but rather from indirect benefits. Females can obtain indirect genetic benefits when potential mates differ in genetic quality that affects their fitness. Females can benefit by mating with high-quality males to obtain those alleles for their offspring. How do females assess the genetic quality of potential mates if they cannot directly observe their genes? One way is by selecting males based on their secondary sexual traits. This idea, that female choice can affect the evolution of male traits, has stimulated much debate and research, starting as early as the nineteenth century.

#### Fisherian runaway and good genes

Perhaps no area in animal behavior has generated as much controversy as indirect fitness benefits via sexual selection, a debate that started with Darwin and his contemporary Alfred Russell Wallace, who independently proposed a theory of evolution based on natural selection. Recall that Darwin proposed two aspects of sexual selection: male-male competition and female (mate) choice. Wallace disagreed vehemently and considered *only* male-male competition to be a selective force ([Wallace 1878](#)). Their argument about the importance of female choice persisted because there was no clear mechanism to explain how mate choice could drive the evolution of secondary sexual traits.

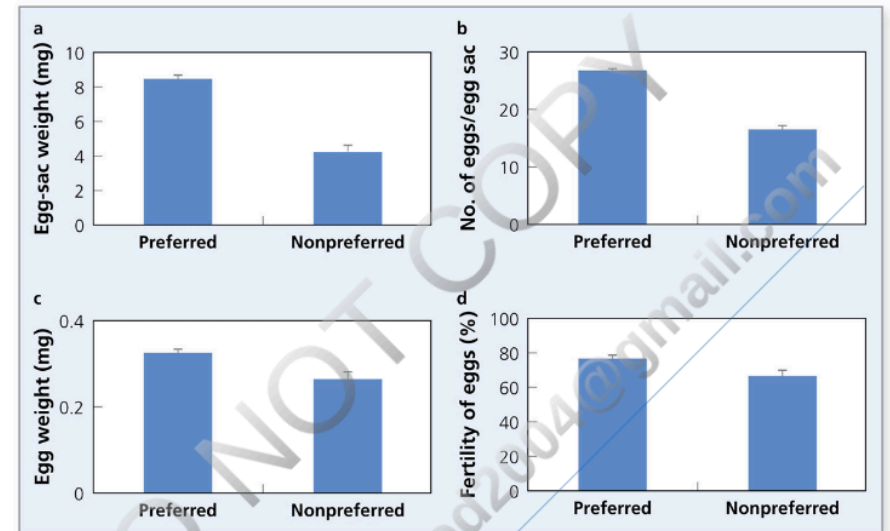
In 1930, Ronald Fisher wrote a milestone paper proposing a genetic explanation for the evolution of exaggerated secondary sexual traits ([Fisher 1930](#)). In his model, Fisher assumed that females select mates based on a particular trait that varies among males. Such a trait could evolve because of (1) its fitness advantage, independent of female choice; and (2) female preference for it. Thus, initially, the trait indicates male quality, because males possessing it have higher fitness and so are more attractive to females. If female preference for a trait and the trait itself have a genetic basis, female offspring will prefer the trait, and male offspring will express it. The intensity of female preference for the trait will increase as long as male offspring have a mating advantage by possessing it.

In sum, the male trait should co-evolve with the female preference and become increasingly exaggerated, what Fisher called a **runaway process**. This would continue until the benefit it provided through sexual selection was outweighed by the disadvantage it entailed through natural selection (e.g., increased predation risk). Russell Lande formalized Fisher's idea into the notion of runaway selection. He showed mathematically how this process could occur through linkage disequilibrium when the genes for the trait and for female preference for the trait are genetically linked ([Lande 1981](#)), even if the trait is unrelated to male fitness. Linkage disequilibrium occurs when the genotype at one locus is not independent of the genotype at another locus.

How common is Fisher's runaway process? The process requires genetic covariation in both the trait and the

How common is Fisher's runaway process? The process requires genetic covariation in both the trait and the mating preference. [Kasey Fowler-Finn and Rafael Rodriguez \(2016\)](#) reviewed dozens of empirical studies that characterized the strength of the genetic covariance between sexual traits and the mating preferences for the trait. Of the 43 studies reviewed, 27 detected a significant genetic covariance. These studies included over 20 species of invertebrates and vertebrates, and involved visual, acoustic, and chemical sexual traits. This review suggests that runaway selection may help to explain the evolution of a variety of sexual traits and mating preferences in diverse taxa.

provide no resources, and so females presumably benefit by obtaining indirect fitness benefits that result in enhanced offspring fitness. The researchers suggest that male pheromones may function as if they convey information about male size, nutritional status, immune function, fertility, or other attributes that affect offspring. Additional work is needed to identify the pheromone(s) involved and how it varies with male phenotype. The fitness benefits of mate choice, like those described here, are starting to influence the management of captive breeding programs ([Applying the Concepts 12.1](#)).



**FIGURE 12.25. Female reproduction.** Mean ( $\pm$  SE) female reproduction. Females mated to their preferred male had (a) larger egg sacs, (b) more eggs per egg sac, (c) higher egg weight, and (d) higher fertility of eggs compared to females mated with their nonpreferred male. (Source: [Koh et al. 2009](#))

### APPLYING THE CONCEPTS 12.1

#### Mate choice in conservation breeding programs

Breeding programs can maintain the viability of captive populations and serve as a source for reintroduction efforts. However, it is crucial to maintain genetic variation and minimize inbreeding. Because captive populations are small, two genetic concerns are the primary focus of breeding programs. First, genetic diversity can decline rapidly as a result of genetic drift, and second, inbreeding can lead to reduced viability of offspring. Both issues can create problems for program success, especially given small captive populations.

Historically, managers have selected breeding pairs based on genetic considerations alone and have hoped that viable offspring would result. Many pairings fail, however, and one factor might be the lack of mate choice. [Cheryl Asa, Kathy Traylor-Holzer, and Robert Lacy \(2011\)](#) noted that litter sizes and offspring survival rates are higher when individuals are allowed to



noted that litter sizes and offspring survival rates are higher when individuals are allowed to select mates compared to when pairings are forced (see, e.g., [Drickamer, Gowaty, & Holmes 2000](#); [Anderson, Kim, & Gowaty 2007](#)).

For instance, Meghan Martin-Wintle and her colleagues investigated the effects of female mate preferences on reproductive success in captive giant pandas (*Ailuropoda melanoleuca*) ([Martin-Wintle et al. 2015](#)). They allowed focal females to interact with a pair of potential mates for one to three days and recorded all interactions. If the female directed greater than 60% of her total behaviors toward one of the males, he was deemed the preferred mate. Subsequently, 25 females were allowed to mate with their preferred mate while 16 were mated to their nonpreferred mate. Over 90% of females mating with a preferred partner produced cubs while only 40% of females mating with a nonpreferred mate produced offspring.

Asa and colleagues suggest that the success of captive breeding programs can be enhanced by incorporating mate choice while taking into account other genetic concerns ([Asa, Traylor-Holzer, & Lacy 2011](#)). For instance, a focal female might be given the option of mating with several genetically acceptable mates. ■

We've seen that females can obtain fitness benefits by preferring to mate with some males over others. In spitting spiders, female egg production and hatch rate were higher when the female mated with a preferred male. One explanation for this outcome is differences in male genetic quality. Another is that the female reduces her reproductive investment based on the quality of her mate. We examine this latter form of sexual selection, which occurs after mating, next.

## 12.4 Sexual selection can also occur after mating

### Learning Objectives

After reading this section, you should be able to

- distinguish sperm competition from cryptic female choice and
- design an experiment to examine each.

Up to now, we have considered aspects of sexual selection prior to copulation. This is only part of the story. Both mate competition and mate choice can occur after gamete transfer. Postcopulatory male competition can occur when females mate with more than one male and the sperm of different males compete to fertilize the eggs, a phenomenon known as **sperm competition** ([Parker 1970](#)). In addition, postcopulatory female choice can occur after gamete transfer when a female influences the fertilization success of sperm from one male over that of others. Both phenomena require that females mate with multiple males, a common behavior that we will address in [Chapter 13](#).

## FEATURED RESEARCH Mate guarding in warblers

One behavior that males can adopt to reduce mate competition and enhance their paternity is **mate guarding**: before and after copulation, a male follows his mate to prevent her from mating with rivals. However, this behavior has obvious costs. The time and energy spent guarding one mate can preclude a male from mating with other females or from acquiring food and other resources.

Helen Chuang-Dobbs and her colleagues studied the effectiveness of mate guarding in black-throated blue warblers (*Dendroica caerulescens*) at the Hubbard Brook Experimental Forest in New Hampshire ([Chuang-Dobbs, Webster, & Holmes 2001](#)). This small (10 g) passerine bird is common in the forests of eastern North America ([Figure 12.26](#)). A single pair will mate and raise offspring together, but females will often mate with other males, and so males risk raising another male's offspring, called **extra-pair young** ([Chuang, Webster, & Holmes 1999](#)). The researchers examined the effectiveness of mate guarding through a combination of observations and an experiment.

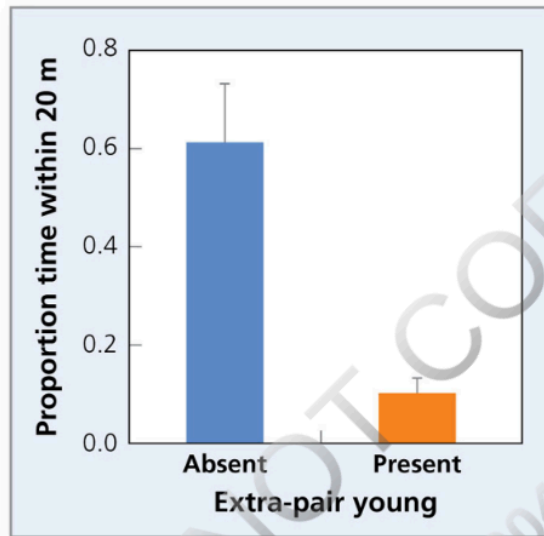


**FIGURE 12.26. Mate guarding.** Male black-throated blue warblers remain close to their mate.

The researchers monitored the breeding behavior of all adults by capturing and color-banding them for identification. In the observational aspect of their study, the research team followed focal males and their mates for up to an hour on days just before egg laying, the period of high fertility for females. Every two minutes, they recorded the distance between individuals and noted how often males followed females or vice versa each time the birds moved to new locations. Evidence of effective mate guarding would be short inter-individual distances and a preponderance of male rather than female follows. The researchers then collected a blood sample from all nestlings for genetic analysis to determine parentage.

Observed males varied in their intensity of mate guarding, and this behavior was associated with variation in the

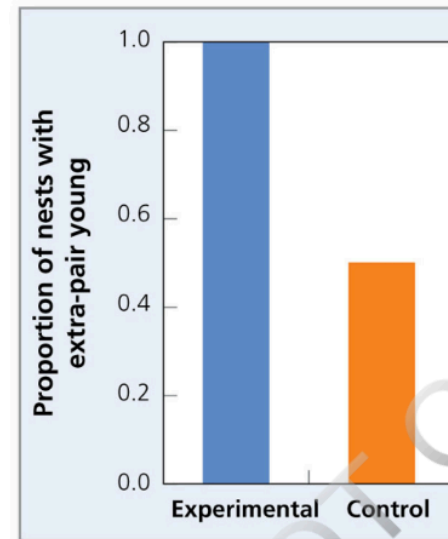
Observed males varied in their intensity of mate guarding, and this behavior was associated with variation in the paternity of offspring. Males that spent more time mate guarding had fewer extra-pair young than those that spent less time mate guarding (as measured by male follows and time spent within 20 m of the female) (Figure 12.27).



**FIGURE 12.27. Intensity of male mate guarding.** Mean (+ SE) proportion of time males spent close to their mate. Males with no ("absent") extra-pair young had spent a greater proportion of their time within 20 m of their mate (mate guarding) than males with extra-pair young ("present") in their nest. (Source: [Chuang-Dobbs, Webster, & Holmes 2001](#))

In the experimental part of their study, the team used a different study plot and removed some males for one hour during the female's fertile period. To do this, they attracted males away from their nests by playing conspecific songs of potential rivals from a speaker located near a territory and placed mist nets next to the speakers to capture the responding birds. Five males were captured and held in captivity, while three others spent most of the hour interacting with the speaker and so spent no time with their mate during the song playback. These eight treatment birds were presumed to exhibit a lower level of mate guarding than the eight control males that were not manipulated. The paternity of treatment and control birds was then compared to determine the effect of reduced mate guarding.

The nests of all experimental males that had been away from their mate for one hour contained extra-pair young, while only 50% of control nests contained such young (Figure 12.28). These findings indicate that mate guarding can be an effective strategy for increasing paternity assurance and thus fitness for males. However, given that control nests did contain extra-pair young, mate guarding does not prevent females from mating with other males. Furthermore, remember that mate guarding comes at a cost: males that spend more time mate guarding have less time to spend seeking matings with other females.



**FIGURE 12.28. Proportion of nests with extra-pair young.** Males that were experimentally removed had a higher proportion of nests with extra-pair young than did controls. (Source: [Chuang-Dobbs, Webster, & Holmes 2001](#))

## FEATURED RESEARCH **Sperm competition in tree swallows**

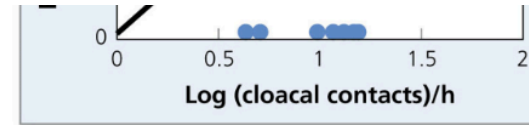
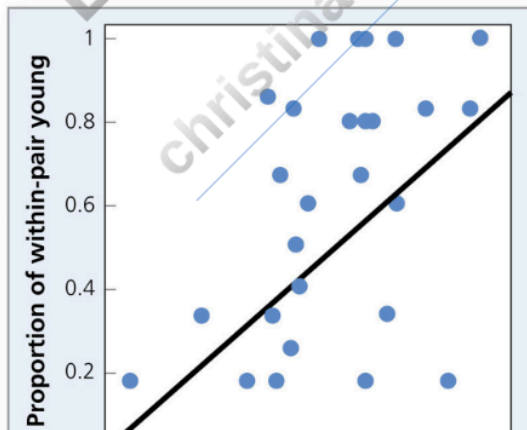
Not all males can continuously guard their mates. If males cannot prevent a female from mating with other males, the sperm of different males may compete to fertilize the eggs. Another way a male can reduce mate competition to enhance his likelihood of success when sperm competition occurs is to swamp a rival male's sperm by mating frequently with a female. Susan Crowe and her colleagues tested the hypothesis that frequent copulation with a mate will enhance male fitness in tree swallows (*Tachycineta bicolor*) ([Crowe et al. 2009](#)). In this species, extra-pair fertilization is common. Males also spend significant time on parental care, so selection should favor behaviors that minimize loss of paternity. Crowe's team predicted that frequent copulation rate would increase paternity for a male.

They tested this prediction on a population of tree swallows at Queen's University Biological Station in Ontario, Canada. Adults and offspring were captured and uniquely marked, and blood samples were taken for genetic analysis. In tree swallows, copulations occur mainly at the nest site and so are relatively easy to observe: males hover over females and make cloacal contact ([Figure 12.29](#)). Previous work has shown that most fertilizations result from copulations that occur during the three days before egg laying ([Lifjeld & Robertson 1992](#); [Lifjeld, Slagsvold, & Ellegren 1997](#)). Consequently, beginning nine days prior to egg laying, each of 43 focal pairs was observed for three hours a day for over two weeks, starting at dawn, when most copulations occur.



**FIGURE 12.29. Swallow copulation.** Males stand on or hover over the backs of females to copulate.

The copulation rate varied among pairs and peaked in the three days prior to egg laying, averaging about five copulations per hour. Paternity analysis revealed that 52% of young were sired through extra-pair copulations. However, an increase in the frequency of copulations by a male increased the percentage of young he sired, as predicted (Figure 12.30). Thus, in this species, males can reduce the likelihood of paternity loss from sperm competition by increasing their copulation frequency.



**FIGURE 12.30. Copulation frequency and paternity assurance.** There is a significant positive relationship between the frequency of copulations (cloacal contacts per hour) and paternity assurance (proportion of within-pair offspring). (Source: [Crowe et al. 2009](#))

High copulation frequency could increase paternity through sperm competition or could act as a type of mate guarding (because frequent copulations prevent other males from mating). Both of these behaviors enhance a male's likelihood of success in mate competition and result in higher rates of fertilization success for a male. Females, however, can also exert mate choice *after* copulation, as we see next.

## Cryptic female choice

As we've seen throughout this chapter, female mate choice prior to copulation is usually obvious: females either do or do not mate with a particular male. Research has also found evidence of female choice after copulation. In species with internal fertilization, a female can mate with multiple males and then influence the fertilization success of sperm from one male over that of others, which is known as **cryptic female choice** ([Thornhill 1983](#)). The usual result is that one male's sperm fertilizes a disproportionate number of her eggs. Why does cryptic female choice exist?

Cryptic female choice will benefit a female that mates with several males that differ in quality. She can enhance the fitness of her offspring by biasing fertilization success in favor of the higher-quality male. One way to evaluate this idea is to examine the fertilization success of males that differ in degree of relatedness to a female. A close relative is a low-quality mate, because such matings often result in low fitness for offspring, a process known as inbreeding depression. In comparison, an unrelated male is a relatively higher-quality mate. Can females affect the fertilization probability of sperm from males that differ in degree of relatedness?

## FEATURED RESEARCH Inbreeding avoidance via cryptic female choice in spiders

Klaas Welke and Jutta Schneider examined whether female orb spiders (*Argiope lobata*) ([Figure 12.31](#)) avoid inbreeding depression by cryptic female choice ([Welke & Schneider 2009](#)). Females occupy webs that are visited by roving males and commonly mate with two males. Each female contains two independent sperm storage organs, and these spermathecae, one on each side of the body, are filled as a result of two separate matings, either by the same male or by different males. Males inseminate females using their paired pedipalps, which are filled with sperm, but use only one pedipalp per mating attempt. In this species, the right pedipalp of a male is always inserted into the right spermathecae of a female, and the same is true for the left side.





**FIGURE 12.31. Orb spider.** Males visit females' webs to mate with them.

Welke and Schneider took advantage of this reproductive morphology to conduct double mating trials. Females were mated with either (1) two sibling males (SS), (2) two nonsibling males (NN), or (3) a sibling and a nonsibling male (switching which one was first, SN or NS). Each male was matched for size and age but had one pedipalp removed so that the pair of males had complementary pedipalps (i.e., one only had the right, and the other only had the left).

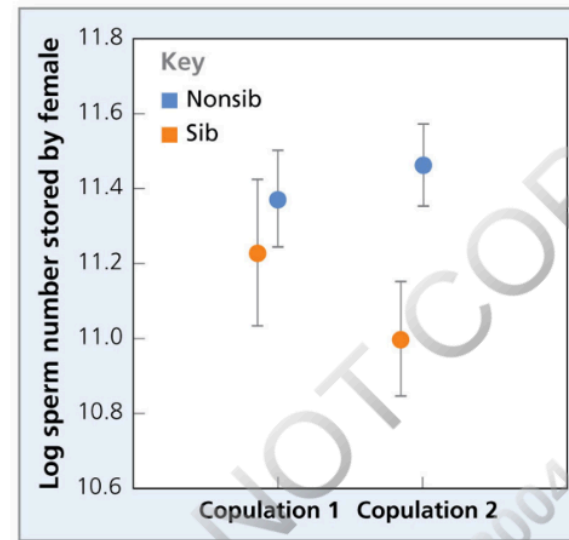
Subjects were offspring of wild-caught females that had laid egg sacs in the laboratory. Hatchlings from each egg sac were kept in separate groups so that siblings (offspring from the same egg sac) and nonsiblings (offspring from different egg sacs) could be identified. Male and female hatchlings were separated until they reached adulthood. Females were placed in individual containers, in which they built a web, while males were kept in separate containers.

Males were introduced to the female's container one at a time, allowed up to one hour to copulate, and then removed. After both males copulated, the researchers estimated the number of sperm transferred to each spermathecae from the first and second mating by sacrificing a subset of females, dissecting the spermathecae, and counting spermatozoa under a microscope. To determine paternity for each male in each treatment, the researchers conducted a second experiment, in which they sterilized one of the males by irradiating him to make his sperm inviable. They could then calculate the proportion of eggs fertilized by each of the two males, because they knew which one was sterilized, and the eggs his sperm fertilized did not hatch.

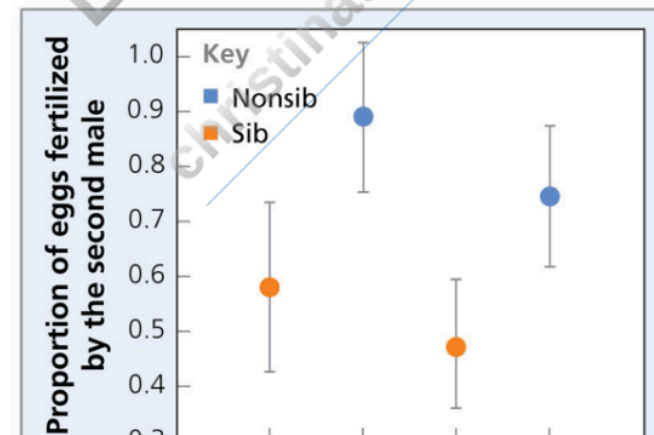
Females mated readily with both siblings and nonsiblings, with no signs of inbreeding avoidance prior to copulation. The number of sperm in the spermathecae from the first male mating did not differ based on his relatedness to the female. However, for the second male, females stored more sperm from the nonsibling than they

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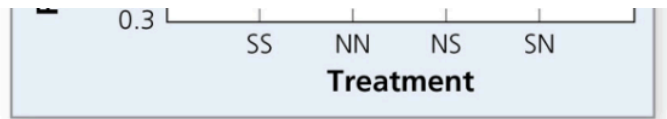
relatedness to the female. However, for the second male, females stored more sperm from the nonsibling than they did from the sibling (Figure 12.32). With respect to paternity, the researchers focused on the proportion of eggs fertilized by the second male. They found that the proportion of eggs fertilized by the nonsibling second male was higher as well (75% versus 48%) (Figure 12.33).



**FIGURE 12.32. Sperm storage.** Mean ( $\pm$  SE) sperm number stored. Females stored more sperm during the second copulation when it came from nonsibling matings (blue) than when it came from sibling matings (orange). (Source: Welke & Schneider 2009)



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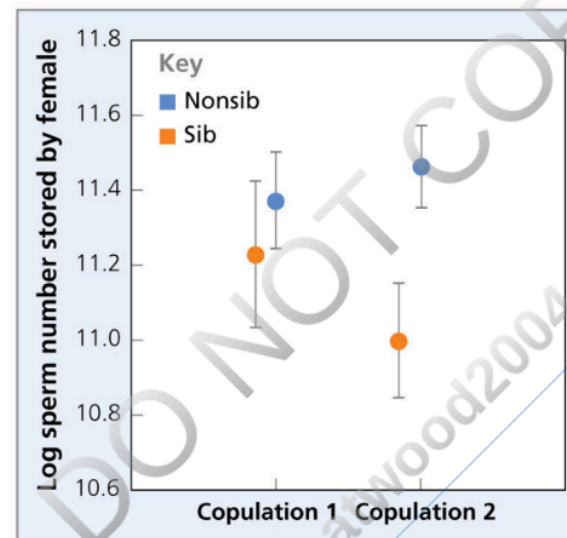


**FIGURE 12.33. Fertilization success of second males.** The mean ( $\pm$  SE) proportion of eggs fertilized by the second male was lower when he was a sibling than when he was a nonsibling. S = sibling; N = nonsibling. (Source: [Welke & Schneider 2009](#))

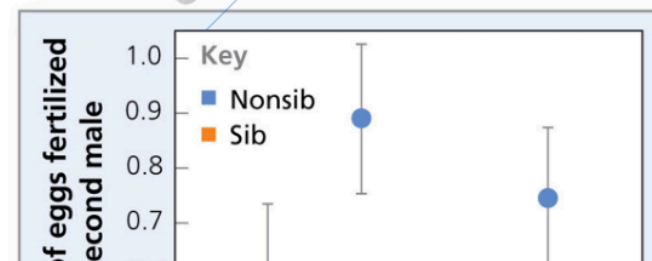
These data demonstrate cryptic female choice by orb spiders. When females mate with two males that differ in relatedness, they store more sperm from the nonsibling male and thus bias paternity toward that male. Both aspects of this choice should reduce inbreeding within a brood.

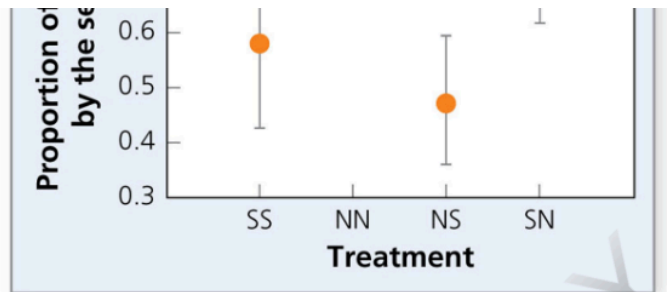
The previous examples illustrate how sexual selection can occur after mating. For males, sperm competition can be intense, and mate guarding and high copulation rates can enhance paternity certainty. Females, too, can affect the outcome of sperm competition via cryptic female choice that biases the fertilization of sperm from one male over that from another. Next, we examine how mate choice by females can favor alternative reproductive tactics in males.

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## 12.5 Mate choice by females favors alternative reproductive tactics in males

### Learning Objectives

After reading this section, you should be able to

- explain the existence of alternative reproductive tactics and
- differentiate between conditional and evolutionary stable strategies.

Throughout the chapter, we have discussed individuals that all use one reproductive strategy to maximize success, such as winning contests over mates, possessing a high-quality territory, or displaying an exaggerated secondary sexual trait. However, as we have seen, not all males are able to win contests, defend high-quality territories, or display exaggerated traits. What do they do? When males cannot effectively compete, selection will favor the

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evolution of alternative strategies that enhance reproduction, and we then observe multiple behavioral phenotypes in a population, known as **alternative reproductive tactics** (Gross 1996; Taborsky, Oliveira, & Brockmann 2008).

Two different behavioral strategies are commonly observed. In the bourgeois tactic, competitive males defend a nest or territory to monopolize its resources for females or else possess traits attractive to females. Typically, the bourgeois males are large, older, and in the best physiological condition. The parasitic tactic, on the other hand, is used by less competitive males to usurp matings from bourgeois males. Several types of parasitic behaviors exist. Satellite males, for example, associate with bourgeois males by remaining near them to intercept females that are attracted to the bourgeois individual. In contrast, sneaker males attempt to avoid detection so that they can quickly enter a bourgeois territory to fertilize eggs being deposited in a nest.

## The evolution of alternative reproductive tactics

How can these two behavioral tactics exist in a population? One explanation states that individuals in the best condition (e.g., older, healthier individuals with high body mass) adopt the bourgeois tactic and defend territories and nests where females reproduce. This tactic often leads to higher fitness but is also more costly to adopt. Individuals in poorer condition can only adopt the parasitic tactic and so obtain some level of reproductive success, even though their fitness, on average, may be lower than that yielded by the bourgeois tactic. These parasitic males are “making the best of a bad situation” until their condition improves, and they can adopt the bourgeois tactic. This flexibility where individuals choose a strategy based on their condition is known as a **conditional strategy** (Kodric-Brown 1986).

A second explanation postulates that the tactics coexist in an evolutionary stable strategy (ESS) that is maintained by frequency-dependent selection (see Chapter 3). Here, neither tactic unilaterally leads to higher fitness, but rather the average fitness of each tactic increases as the tactic becomes less common. This idea makes sense when we think about the parasitic tactic. These males do not pay the costs associated with the bourgeois tactic of attracting a mate or defending a resource. They can thus parasitize more individuals and obtain high fitness when there are many more bourgeois males in the population than parasites. However, if too many males in a population exhibit the parasitic tactic, they will, on average, have low fitness, because there will then be too few bourgeois males to parasitize. This idea predicts equal fitness for the tactics when they coexist as an ESS (Gross 1996). Let's see how these explanations have been tested.

## FEATURED RESEARCH Conditional satellite males in tree frogs

Male frogs produce advertisement vocalizations near ponds and streams to attract females. Females prefer to mate with those males that produce the most energetic calls (the loudest and at the highest rate) and calls of the lowest frequency. Typically, only large males can produce the lowest-frequency sounds (Gerhardt 1987).

Sarah Humfeld examined male reproductive behavior in green tree frogs (*Hyla cinerea*) in southeastern Missouri (Humfeld 2008). In this population, males exhibit both a bourgeois calling tactic and a parasitic satellite tactic. In the first, they call to attract females. In the second, a satellite male takes up residence near a calling male but

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the first, they call to attract females. In the second, a satellite male takes up residence near a calling male but remains silent, presumably to intercept females attracted to the caller. Humfeld noticed that some males use both tactics. Could this represent a conditional reproductive strategy? Humfeld's hypothesis made two predictions: (1) males differ in attractiveness to females, and those that produce unattractive calls are more likely to be satellites; and (2) satellite males should exhibit the same call preference as females—that is, both should be attracted to males that exhibit the lowest-frequency calls.

#### Video: Green tree frog calling and satellite male getting mating

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Video: Green tree frog calling and satellite male getting mating

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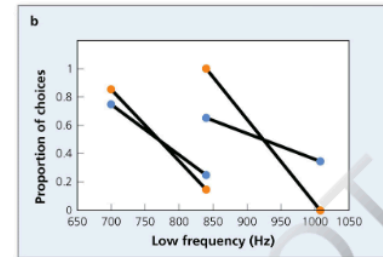
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To test these predictions, Humfeld characterized the advertisement calls of males in the wild. Each male in the population was observed and assigned a status of either bourgeois calling male or silent satellite. She recorded 20 consecutive calls and then captured, measured, and marked each male. To obtain calls from satellites, she removed the nearest caller, which induced the satellite to begin calling, and then she recorded his calls. Humfeld found that bourgeois calling males were larger, in better condition, and produced lower-frequency calls than satellites—data that support the first prediction: satellites produce less attractive calls.

Next, Humfeld determined the vocal preference of females and satellite males. To do this, she created pairs of synthesized calls that were identical except for the lowest frequency they reached. The lowest frequencies of one pair were 700 Hz and 840 Hz, and those of the other pair were 840 Hz and 1,120 Hz. Humfeld captured females and placed them individually in a choice arena, covered with a dark cloth and away from all natural populations of calling males. She placed two speakers on either side of the arena and recorded the movement of the female toward one of the speakers, an index of her vocal preference. Then, to determine how different male calls affect satellite males, Humfeld repeated the experiment, but this time with individual satellites in the arena. She found that females and satellites both strongly preferred those male calls with the lowest frequencies, as predicted (Figure 12.34).

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**FIGURE 12.34. Female and satellite male choices.** (a) Green tree frog. (b) Both females (orange) and satellite males (blue) preferred the call with the lowest low-frequency peak in two experiments that differed in the calls presented. Lines connect the two calls of an experiment. (Source: Humfeld 2008)

Humfeld concluded that male green tree frogs adopt a conditional strategy. Females prefer large males in good condition, the only males that can produce low-frequency calls. Small, perhaps younger, males call when away from an attractive male, but because of their size and condition, they cannot produce attractive calls, and so when an attractive male is nearby, they adopt a satellite strategy and remain silent but stay close to that male. This behavior should increase their encounters with females until they attain a larger size. The experiment did not yield data on male fertilization success, and so the relative fitness of the different strategies is unclear. However, the data suggest that if satellite males attempted to attract females by calling alone, they would be unsuccessful.

## FEATURED RESEARCH ESS and sunfish sneaker males

As we just saw, testing hypotheses about the evolution of alternative reproductive tactics is challenging because it is often difficult to quantify fitness for different mating tactics. However, the advent of molecular techniques has allowed scientists to establish paternity and thereby understand the fitness consequences of these tactics.

Oscar Rios-Cardenas and Michael Webster examined the mating behavior and reproductive success of male pumpkinseed sunfish (*Lepomis gibbosus*) in a small (4 ha) pond at the Huyck Preserve in upstate New York (Rios-Cardenas & Webster 2008). Pumpkinseed sunfish are medium-sized (15–20 cm in length) freshwater fish that are common in ponds and streams throughout North America (Figure 12.35). Some male sunfish, called parentals

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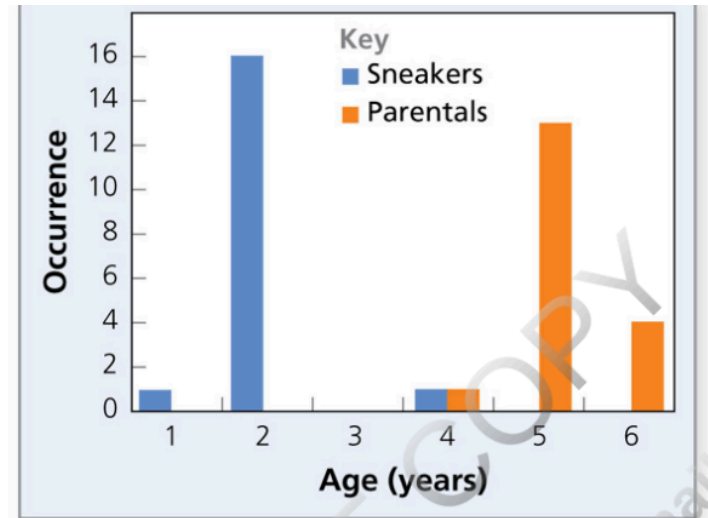
(i.e., those that adopt a bourgeois tactic), defend nests in breeding territories and provide parental care for the eggs there. Females approach these males and spawn at a nest site within the territory. Parasitic sneaker males do not defend territories but instead intrude while a parental male is spawning with a female in an attempt to fertilize eggs as they are laid.



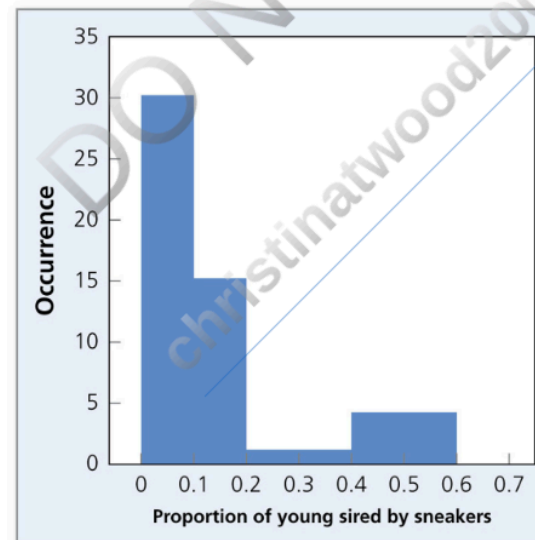
**FIGURE 12.35. Pumpkinseed sunfish.** These fish are found in all the Great Lakes and are popular with anglers.

Over a period of three years, the researchers mapped the location of all active nests. When a spawning event occurred, the researchers captured nesting males, females, any sneakers involved in the spawning attempt, and all subsequent developing eggs. Tissue samples were taken from the adults and eggs for genetic analysis of paternity. Males were weighed, and their age was determined based on scale morphology.

The researchers observed 435 active nests, 60 spawning events, and 26 sneaker intrusions. They found that sneaker males were younger and smaller than parentals; most sneaker males were about two years old, while parental males were at least four years of age (Figure 12.36). On average, parental males sired about 85% of the offspring in their nest, and sneakers sired 15% (Figure 12.37). At first glance, parental males might seem to have higher fitness than sneakers, but sneakers are much rarer in the population than parentals. In fact, the researchers estimated that sneaker males represent only about 15% of the population. Because the reproductive success of sneakers is in proportion to their abundance in the population, the two strategies actually have equal reproductive fitness.



**FIGURE 12.36. Male ages.** Relative frequency of sneaker and parental males by age. Sneaker males were younger and smaller than parental males. (Source: Rios-Cardenas & Webster 2008)

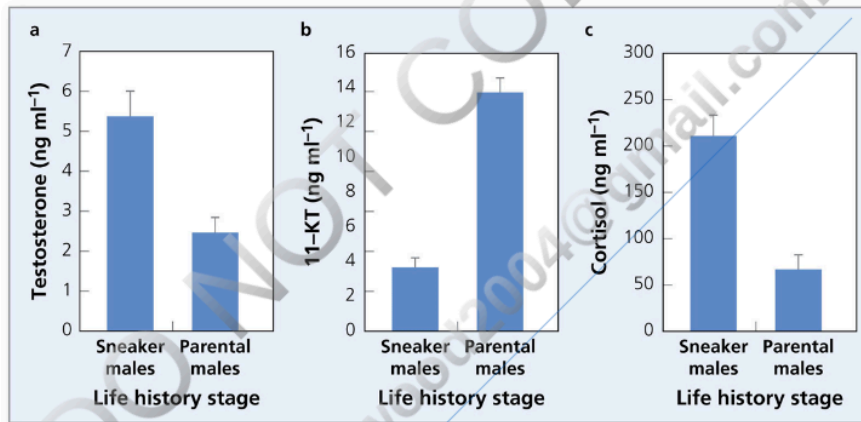


**FIGURE 12.37. Proportion of young sired by sneakers.** Frequency of reproductive success by sneakers. Most sneaker males sired less than 10% of eggs in a nest. (Source: Rios-Cardenas & Webster 2008)

Most sneaker males sired less than 10% of eggs in a nest. (Source: [Rios-Cardenas & Webster 2008](#))

The researchers concluded that in this population, the two strategies are in an ESS. About 15% of individuals mature rapidly at two years of age and adopt the sneaker tactic. The remainder continue to grow and mature at four years of age, when they begin to compete for territories.

Additional work is required to understand how this reproductive decision occurs, but perhaps physiology plays a role. Rosemary Knapp and Bryan Neff studied closely related bluegill sunfish (*Lepomis macrochirus*) and found that parental and parasitic males exhibited different hormone profiles ([Knapp & Neff 2007](#)). Males that had adopted the parasitic tactic had higher testosterone and cortisol and lower 11-ketotestosterone levels than parental males ([Figure 12.38](#)). This finding suggests that hormones may regulate the adoption of different reproductive tactics in sunfish.



**FIGURE 12.38. Hormone profiles.** Mean (+ SE) hormone levels of males. Sneaker and parental males exhibited different levels of (a) testosterone, (b) 11-ketotestosterone, and (c) cortisol. (Source: [Knapp & Neff 2007](#))

The examples on tree frogs and sunfish illustrate that mating behavior is complex and can involve a variety of tactics by males. In the final section, we examine how the decisions of others can also influence mating behavior.

### Video: Pumpkinseed male spawning and protecting nest

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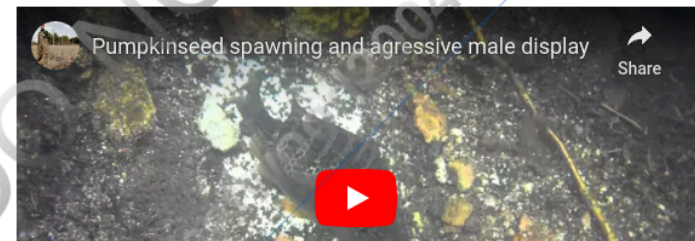
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Video: Pumpkinseed male spawning and defending nest



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## 12.6 Mate choice is affected by the mating decisions of others



## Learning Objectives

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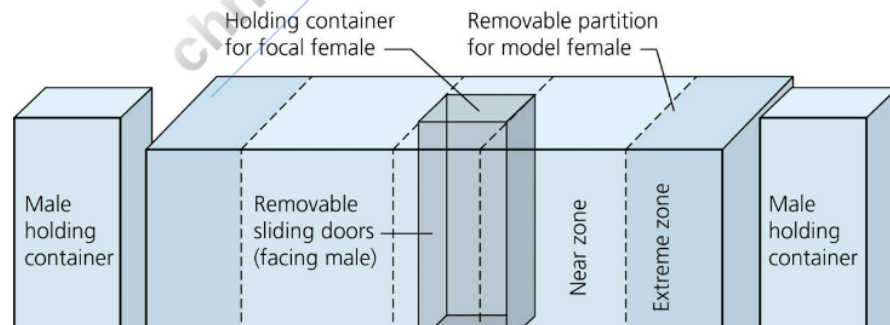
- describe the potential benefits of mate choice copying and
- design an experiment to test mate choice copying.

Throughout the chapter, we have assumed that the mate choice decisions of individuals are independent. Yet mating for many species takes place in a social environment, where individuals can observe and copy the mating decisions of others, a behavior known as **mate choice copying**, or nonindependent mate choice. We illustrate this behavior with examples from fish and fruit flies.

## FEATURED RESEARCH Mate copying in guppies

The first experimental evidence of mate choice copying comes from guppies (*Poecilia reticulata*), small freshwater fish native to Trinidad. Recall that males are brightly colored, with areas of orange, black, and iridescence coloration on their body (Figure 12.10). Lee Dugatkin examined whether females copied the mate choice of other females (Dugatkin 1992).

To answer this question, he placed a focal female in a clear Plexiglas container in the center of an aquarium. He then placed males, matched for size and overall coloration, into chambers on either side of the aquarium. Dugatkin first allowed a focal female to choose one of the males. In guppies, the amount of time a female spends near a male is a good indicator of her mate preference. Next, he arranged the aquarium so that a different female (the model) was now near the nonchosen male. This was done to simulate her “choosing” this male as a mate (Figure 12.39). During this time, the model female and male interacted with typical courtship behaviors, which the focal female could view. The model was then removed, and the focal female was released and allowed to swim freely for ten minutes. Dugatkin again recorded the amount of time the focal female spent next to each male.



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**FIGURE 12.39. Choice test design.** The test apparatus had separate containers for males and movable doors that were used to adjust what the female viewed. (Source: LaFleur, Lozano, & Sclafani 1997)

Of 20 focal females, 17 spent significantly more time next to the male that had been near the model female. These females switched their mate choice preference to copy the mate choice of the model female. In this species, mate choice is not always independent; instead, females will copy the mate choice of others they observe.

## FEATURED RESEARCH Mate copying in fruit flies

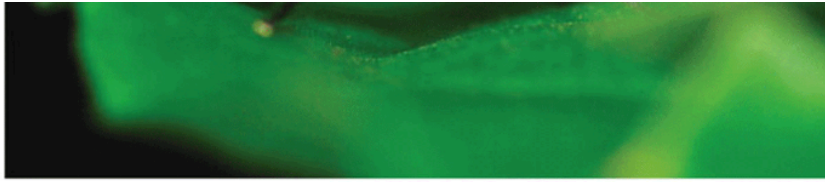
Mate choice copying has now been documented in many species, but most often in vertebrates (Hoppitt & Laland 2008). Recently, Frédéric Mery and colleagues examined this behavior in fruit flies (*Drosophila melanogaster*) (Mery et al. 2009) (Scientific Process 12.2). The research team gave females a choice of males that were made to differ in quality by raising some on a rich-food medium that contained 100% of standard nutrients (high-quality males) and others on a poor-food medium that contained only 25% of standard nutrients (low-quality males). The researchers then conducted a three-phase experiment in a small Plexiglas box. In the pretest, females were allowed to choose between a high-quality and a low-quality male, and they spent more time with the high-quality male. Next, half the females saw a model female with the high-quality male, and the others saw a model female with the low-quality male. In the posttest, females were again allowed to choose between the high-quality and low-quality males. The behavior of the treatment females differed. Those that saw a model with the high-quality male again chose that male, as expected. However, those that saw a model with the low-quality male now spent significantly more time with him—that is, they exhibited mate choice copying. Why might females make this switch? We examine that next.

### SCIENTIFIC PROCESS 12.2

#### Mate copying in fruit flies



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Research Question: *What factors affect the mating behavior of female fruit flies?*

### Hypothesis:

Observations of the mating decisions of others will affect the mating decisions of female fruit flies.

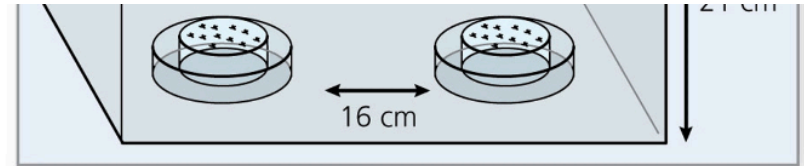
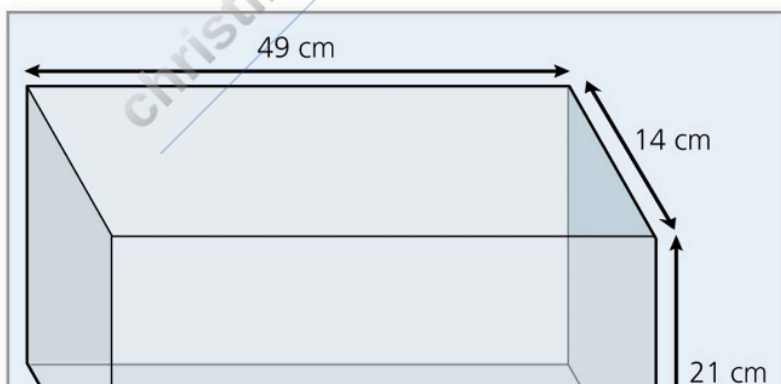
### Prediction:

Female fruit flies will change their mate preference after observing another female associate with a previously nonpreferred male.

### Methods:

The researchers:

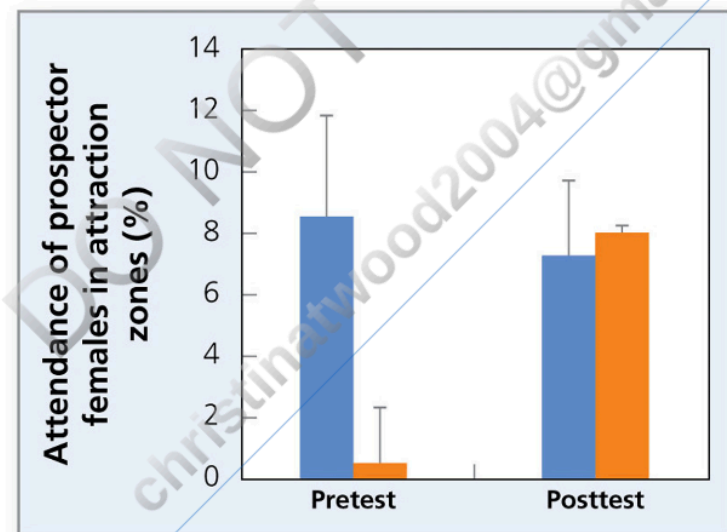
- Created groups of high-quality males (fed nutrient-rich food) and low-quality males (fed nutrient-poor food)
- Conducted a female mate choice trial with one high- and one low-quality male (pretest)
- Allowed half the females to then observe a model female next to the high-quality male, while the other observed a model female next to the low-quality male
- Repeated the mate choice trials (posttest)



**FIGURE 1.** Experimental arena. Males were restrained under lids that allowed females to obtain visual and olfactory information. (Source: [Mery et al. 2009](#))

### Results:

- In the pretest, females spent significantly more time near the high-quality male.
- In the posttest, females that observed a model female with the low-quality male now spent more time near the low-quality male.



**FIGURE 2.** Posttest female behavior. Mean (+ SE) attendance of females, with blue bars denoting high-quality males and orange bars denoting low-quality males. In the posttest, the attractiveness of the high-quality male did not change. However, the attractiveness of the low-quality male increased significantly. (Source: [Mery et al. 2009](#))

### Conclusion:

Female fruit fly mating behavior is affected by observing the mating decisions of other females.

### Evaluate

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## The benefit of mate copying

When a female copies the mating behavior of another female, it might be making a poor choice (one that results in low fitness) if the observed female mated with a low-quality mate. Why should an individual copy the mate choice of another individual rather than making the decision on its own; that is, how can mate copying behavior evolve?

One answer comes from a simple model (Nordell & Valone 1998). If a female has the option of mating with two

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One answer comes from a simple model (Nordell & Valone 1998). If a female has the option of mating with two males that differ in quality, she will have higher fitness by mating with the higher-quality option. However, it may be difficult for a female to determine which male is of higher quality if the males are similar or if she has little experience discriminating between males. In the absence of other information, she must select one at random and so will have only a 50% chance of making the best decision. Alternatively, she can observe another female and copy *her* mate choice. If the observed female is a better discriminator, the copying female will have a higher chance of selecting the higher-quality male. If not, she is no worse off.

This model predicts that mate copying should be observed only when discrimination is difficult—that is, when the males are matched for quality. In guppies, for instance, females prefer males with the most orange coloration, and females mate copy when males are matched closely for color. When males are very different in color, female copying is rarely observed (Dugatkin & Godin 1993). In addition, if discrimination ability increases with age and experience, the model predicts that young females should mate copy more often than older females, a tendency that has been demonstrated in guppies (Dugatkin & Godin 1993).

## FEATURED RESEARCH Nonindependent mate choice by male mosquitofish

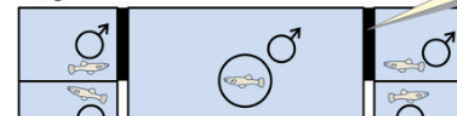
Now we know that female mate choice is affected by the mating decisions of other females. Is the same true for males? Recall that males compete with one another to fertilize eggs, often by sperm competition inside a female's reproductive tract. We might therefore predict that males should try to avoid mating with females they have recently seen mate.

Bob Wong and Miranda McCarthy asked: Does the risk of sperm competition affect mate choice in male eastern mosquitofish (*Gambusia holbrooki*)? They conducted a three-stage experiment using a standard two-choice test with three aquaria (Figure 12.40) (Wong & McCarthy 2009). In the first stage, Wong and McCarthy examined the preference of focal males for two randomly selected females. In the second stage, the focal male was constrained, and a rival male was placed next to each female. Here, the researchers could control whether the focal male observed these other males. Half the focal males saw a rival only near the female he had preferred in the first phase of the experiment while the others saw a rival only next to the female he had not preferred in the first phase. In the final stage, the rivals were removed and the focal male was again allowed to associate with both females.

### Stage 1:



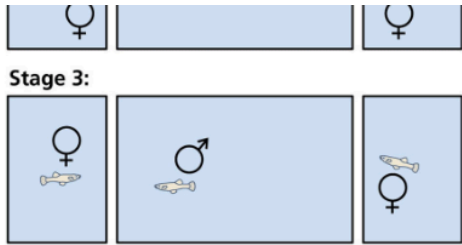
### Stage 2:



One of these partitions was removed to allow the focal male to see the rival.

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**FIGURE 12.40. Male preference experimental setup.** Each experiment consisted of three stages. Stage 1 measured male preference, Stage 2 allowed males to see a rival next to a female, and Stage 3 measured male preference again. (Source: [Wong & McCarthy 2009](#))

Males consistently preferred the same, larger female in Stages 1 and 3 after observing a rival near their unpreferred female in Stage 2 ([Figure 12.41](#)). However, males that observed a rival near their preferred female in Stage 2 tended to spend less time near that female in Stage 3 ([Figure 12.42](#)). These results show that males have a mating preference for larger females and that their preference of mates is influenced by observing the choice of other males. They will spend less time near a preferred

## CHAPTER SUMMARY AND BEYOND

The study of mating behavior is organized around the concept of sexual selection—differential reproduction as a result of competition to mate and selective mate choice. Sexual selection theory assumes that, in general, male fitness increases most strongly with the number of sexual partners, whereas female fitness increases more by selecting mates that provide resources or genetic benefits. Therefore, males will often compete for access to females, and females will be choosy in their selection of mates. Sexual selection also explains the evolution of elaborate secondary sexual characteristics and courtship displays, and both are the focus of much research ([Jones & Ratterman 2009](#)). [Barry and Kokko \(2010\)](#) summarize why male mate choice is rare in most species. Reevaluation of Bateman's seminal work prompted significant theoretical critiques, but many of his basic conclusions remain valid ([Tang-Martinez & Ryder 2005](#)). More proximate studies of mating behavior have focused on how genes regulate the development of traits in one sex but not the other ([Williams et al. 2008](#)) and on the neural activation involved in sexual selection ([Hoke, Ryan, & Wilczynski 2010](#)). Although sexual selection is typically used to explain traits within a species, it can promote speciation as well ([Servedio & Boughman 2017](#)).

Females can benefit from mate choice by obtaining direct material benefits when selecting males that provide nutrient-rich nuptial gifts prior to mating or access to a territory that provides abundant resources ([Gwynne 2008](#)). Females can also benefit by selecting mates that provide indirect genetic fitness benefits. One way this can occur is through the existence of a genetic covariance between genes that affect female mating preferences and the sexual trait in males they prefer. Alternatively, females can benefit indirectly by selecting males that possess good genes that will be passed on to her offspring. Additional work has focused on understanding the indirect benefits of mate choice, including how often genetic covariances or good genes explain mating preferences and sexual traits (e.g., [Prokop et al. 2012](#); [Prum 2012](#); [Greenfield et al. 2014](#)). Another focus involves female choice based on immune system function and heterozygosity (e.g., [Garcia-Navas, Ortega, & Sanz 2009](#)). One area of interest is the major histocompatibility complex, genes that encode for proteins involved in the immune system response to pathogens ([Strandh et al. 2012](#)).

Sexual selection also occurs after mating. Sperm from different males often compete to fertilize eggs within the female reproductive tract. Female physiology can bias the outcome of such competition, a phenomenon known as cryptic female choice, which can reduce fitness costs associated with inbreeding depression. [Firman, Gasparini, Manier, and Pizzari \(2017\)](#) provide a review of empirical work on cryptic female choice. When males cannot successfully compete for females, selection will favor alternative mating tactics; common examples in many taxa are satellites and sneakers. Ongoing work has attempted to determine whether such tactics yield the same fitness as those used by competitive males ([Taborsky, Oliveira, & Brockmann 2008](#)) and on how alternative mating tactics can evolve ([Engqvist & Taborsky 2016](#)).

In many species, the choice of a mate is affected by the mating decisions of others because mate

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## CHAPTER 11

# Habitat Selection, Territoriality, and Aggression

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 11.1 [Resource availability and the presence of others can influence habitat selection](#)
- 11.2 [Individual condition and environmental factors affect territoriality](#)
- 11.3 [Hormones influence aggression](#)
- 11.4 [Game theory models explain how the decisions of opponents and resource value affect fighting behavior](#)

### Features

#### Scientific Process

- 11.1 [Ideal free guppies](#)
- 11.2 [Conspecific attraction in grasshoppers](#)

#### Applying the Concepts

- 11.1 [Conspecific attraction and conservation](#)
- 11.2 [Human aggression, testosterone, and sports](#)
- 11.3 [Reducing duration and intensity of piglet fights](#)

#### Toolbox

- 11.1 [The hawk-dove model](#)

#### Quantitative Reasoning

- 11.1 [Trout territoriality](#)

A few years ago, we returned from a hike to find a northern mockingbird (*Mimus polyglottos*) vigorously pecking at our car's side-view mirror ([Figure 11.1](#)). We watched for a while, trying to understand this seemingly odd behavior. We realized this bird probably perceived its reflection as a rival threat that required active aggression.

Once we placed a shirt over the mirror, the behavior stopped. Our observation was not that unusual; in fact, researchers often use mirror reflections to study aggressive behavior (e.g., [Kusayama, Bischof, & Watanabe 2000](#)).



**FIGURE 11.1.** Mockingbird and mirror. A mockingbird attacks its mirror image, a perceived rival, to defend its territory.

Many animals, like the mockingbird we observed, defend territories, particularly during the breeding season. Before breeding, however, many individuals must select a habitat in which to settle. In this chapter, we'll see that habitat quality and the presence of conspecifics play major roles in habitat selection. The presence of another individual means that resources will be used by multiple individuals and that competition in these areas may be high. Yet the presence of a rival may also indicate that a habitat is of high quality. We'll also see that once an individual has settled in a habitat, territorial defense can provide preferential access to food or mates. However, aggressive interactions are costly, and so not all individuals can successfully defend a territory. Next, we examine how hormones influence aggressive behavior. Finally, we discuss how game theory models are used to understand the tremendous variation observed in the intensity and duration of aggressive contests over resources.

### Video: Bird attacking car mirror

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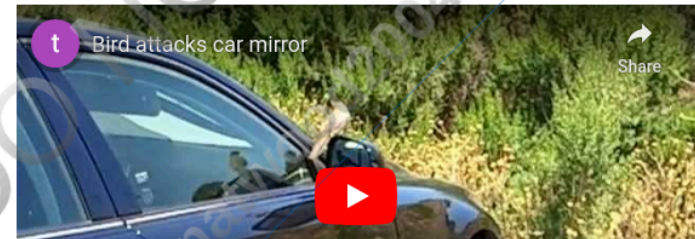
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### 11.1 Resource availability and the presence of others can influence habitat selection



## Learning Objectives

After reading this section, you should be able to

- summarize the five assumptions and two predictions of the ideal free distribution model,
- identify conspecific attraction, and
- distinguish between Allee effects and conspecific cueing as mechanisms to explain conspecific attraction.

Recall that in [Chapter 1](#), we examined a hypothetical situation in which there was variation in the number of robins in yards: some yards had many robins, while others had few. In nature, such variation in the density of individuals in different habitat locations is common. Two factors help explain much of this variation: the amount of resources and the number of competitors in a habitat. Resource availability is an important aspect of habitat quality, and the number of competitors in a habitat affects the level of competition for those resources. Let's see how researchers have examined the importance of these factors to explain distributions of animals.

## The ideal free distribution model

Steve Fretwell and Henry Lucas developed the **ideal free distribution (IFD) model** to explain how animals distribute themselves among habitats ([Fretwell & Lucas 1969](#)). The model's name comes from its assumption that animals act in an "ideal" manner, in that they select habitats that maximize survival and reproduction, and are "free" to enter any habitat.

The model contains five assumptions:

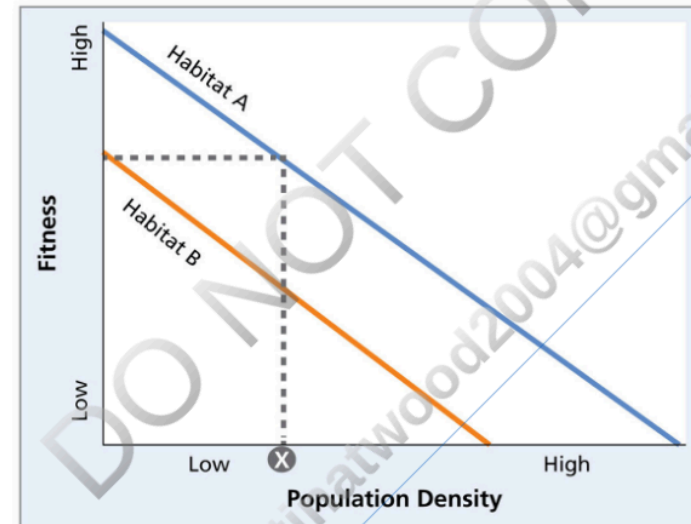
1. Individuals attempt to maximize their fitness when settling in a habitat.
2. Habitat locations differ in the resources they contain.
3. The fitness of individuals in a habitat decreases as more individuals settle there because of increased competition for resources. In other words, fitness is negatively density dependent.
4. Individuals have equal competitive ability and can accurately assess the fitness payoffs of each habitat.
5. Individuals are free to move between habitats at no cost.

The model then makes the following predictions:

**Prediction 1:** Individuals will settle in habitats based on the relative fitness payoffs of those habitats: the number of individuals in each habitat will be proportional to habitat quality, resulting in more animals settling in higher-quality habitats.

**Prediction 2:** In the end, all individuals will have the same fitness no matter where they settle.

We can understand the logic of these predictions by examining two hypothetical habitats, or habitat patches, of high and low quality ([Figure 11.2](#)). Imagine a situation in which individuals settle sequentially in these habitats. The first few individuals should settle in the high-quality habitat because this will yield the highest fitness. However, as more and more individuals enter the high-quality habitat, the fitness of each individual will decline because of increasing competition for resources, producing a negative relationship between the number of individuals in a habitat and their fitness. At some point, the fitness payoff will be higher for an individual settling in the poor-quality habitat, so a new settler should go there, and additional settlers should then select both of these habitats equally.



**FIGURE 11.2. Ideal free distribution model.** Consider two habitats, A and B. Habitat A (blue line) is the higher-quality habitat because it yields the highest fitness for any given population density. As individuals first arrive, all individuals should select Habitat A. After more than X individuals arrive, they should settle equally in both habitats.

This model also allows us to make predictions about the relative number of individuals in each habitat. If habitat quality is determined by resources, the model predicts that the number of individuals in a habitat will be proportionate to the resources available. If one of the habitats in our example contains twice the resources of the other, twice as many individuals should settle there. If the resources differ by a factor of ten, so will the number of individuals. In this way, each individual obtains the same fitness no matter which habitat it settles in. During the settling process, individuals are always free to move to a higher-quality habitat if one is available. However, once all individuals settle, none can do better by moving to another habitat. Let's look at two tests of these predictions.

all individuals settle, none can do better by moving to another habitat. Let's look at two tests of these predictions.

## FEATURED RESEARCH The ideal free distribution model and guppies

The IFD model is easiest to test at a small spatial scale; therefore, numerous tests have used small food patches. At this smaller scale, patch quality (i.e., habitat quality) can be manipulated by changing food density or provisioning rate. Mark Abrahams did this when he tested the model using guppies (*Poecilia reticulata*) (Abrahams 1989). Abrahams created two food patches using flasks filled with water that delivered food (fly eggs) to two feeding bars, or patches, on opposite sides of an aquarium. He modified the quality of each patch by changing the number of eggs in each flask. In this way, the relative patch quality varied from equal (1:1 ratio) to highly skewed (1:9 ratio). He then placed ten individuals of the same sex in the aquarium and fed them at three distinct times each day using the same relative patch qualities. In each trial, he recorded the number of fish at each patch (Scientific Process 11.1).

### SCIENTIFIC PROCESS 11.1

#### Ideal free guppies



Research Question: *How do guppies distribute themselves among food patches?*

#### Hypothesis:

Food delivery rate and number of competitors will affect the distribution of individuals among food patches, as outlined by the IFD model.

#### Prediction:

Individuals will distribute themselves so that all obtain equal food intake rates. Their relative abundance will match the relative rate of food delivery.

#### Methods:

The researchers:

- Conducted trials using groups of ten males or ten females in 90 L aquaria. Feeders (Erlenmeyer flasks with a stir rod to keep fly eggs in the water solution) were placed on two sides of the aquarium with a piece of tubing creating a horizontal feeding bar. The presence of different amounts of food in each flask created patches of different quality but kept the overall total food the same across treatments.
- Conducted three trials per day (one in the morning, one at noon, and one in the evening) using the same relative patch qualities
- Counted the position of the guppies (left feeder, right feeder, or not feeding) every 30 seconds for 24 minutes per trial

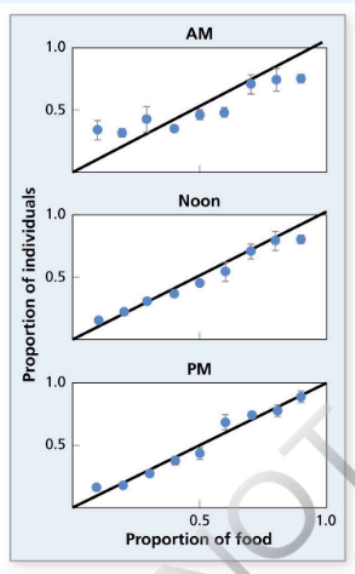


**FIGURE 1.** Experimental tank. Feeders on each side create two feeding patches. A trough under the feeding bar collects extra food. (Source: Abrahams 1989)

#### Results:

- The distribution of male and female fish was strongly affected by the amount of food in a patch.
- In the morning trial, fewer fish than predicted used the patch with more food.
- In the noon and evening trials, the distributions matched the IFD prediction.

- Within a patch, the feeding intake rate of individuals was similar, as the model assumed.



**FIGURE 2. Patch use.** The proportion of individuals at the left feeder versus the proportion of food available at that feeder for the morning, noon, and afternoon trials. (Source: [Abrahams 1989](#))

#### Conclusion:

Guppies distributed themselves according to the predictions of the IFD model once they had time to learn the distribution of food.

#### Evaluate

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The IFD model predicts that the fish should distribute themselves among the patches in the same ratio as the food delivery ratio. Abrahams found that the model accurately predicted the distribution of fish in the trials held later in the day, but not their distribution in the first trial of the day. Why? Apparently, it took the fish some time each day to learn the relative qualities of the patches. Abrahams also quantified individual feeding rates for a smaller sample of fish by counting the number of eggs eaten by each individual at a patch. He found that all fish had the same feeding intake rate and saw no evidence of unequal competitive ability—a finding that would have violated an assumption of the model. Abrahams's results support the IFD model, demonstrating how resources and competition affect the distribution of individuals among patches.

The IFD model has been very effective in predicting and explaining variation in the number of individuals in food patches. Can the model also explain habitat selection over larger geographic scales and longer time scales? Our next study provides the answer.



aggressively for a territory.

## 11.2 Individual condition and environmental factors affect territoriality

### Learning Objectives

After reading this section, you should be able to

- distinguish between a home range and a territory and
- explain how variation in body condition among individuals affects territoriality.

When animals settle in an area, they can establish a **territory**, an area defended to obtain the exclusive use of the resources it contains, such as food, nesting sites, or access to potential mates. Territorial defense provides exclusive use of resources but also requires that animals expend effort to defend these resources from rivals. Territories differ from **home ranges**, which are areas of repeated use that are not defended. The home ranges of many individuals can overlap, while territories do not. Territory defense requires physical effort: it takes both time and energy to chase off intruders. Can all individuals defend a territory?

### FEATURED RESEARCH Body condition and territoriality in damselflies

Aggressive behaviors involved in territorial defense require substantial effort, and so only individuals in good body condition may be able to acquire and defend a territory. Body condition can be measured by body mass, body size, or measures of fat, which indicates extra energy storage that could be used in intense behavioral interactions. Odonates (dragonflies and damselflies) defend territories and are easy to observe and manipulate; consequently, they have often been the focus of studies of territoriality. For example, Jorge Contreras-Garduño and colleagues studied how the physiological status of male damselflies affects their ability to acquire and defend a territory.

The researchers studied territorial behavior in the American rubyspot (*Hetaerina americana*), a damselfly found throughout North America near sunny riverbanks. Adults emerge from a pupa and feed on mosquitoes. After several days of feeding and development, individual males reach sexual maturity and then fight for a territory, a perching site. Territory ownership is determined in aerial contests, which can be as short as three seconds or as long as two hours (Córdoba-Aguilar & Cordero-Rivera 2005). Males that cannot gain a territory simply search for females in their home range, but this tactic results in very limited mating success. What determines whether a male gains a territory? Territory disputes can be energetically expensive, and so the research team examined whether territorial males had higher fat reserves than nonterritorial males. Fat serves as fuel for energetically costly behaviors such as fighting, and so larger reserves of fat should allow individuals to fight longer and more

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### Video: Male American rubyspot fighting with tethered intruder

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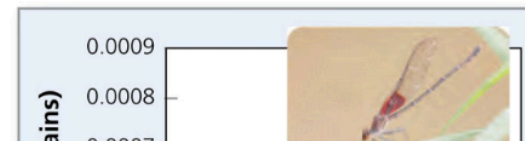


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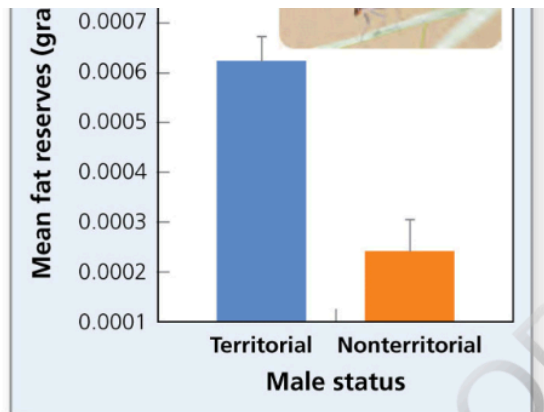
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The researchers first compared the fat content of territorial and nonterritorial males of similar age from the Xochitepec River in Mexico (Contreras-Garduño, Canales-Lazcano, & Córdoba-Aguilar 2006). To measure body fat content, they weighed the body both before and after extracting the fat. The difference yielded the fat mass of a male. They found that territorial males had much higher fat reserves than nonterritorial males (Figure 11.11), indicating that territorial males did indeed have higher potential energy reserves. But are these fat reserves used to maintain a territory?



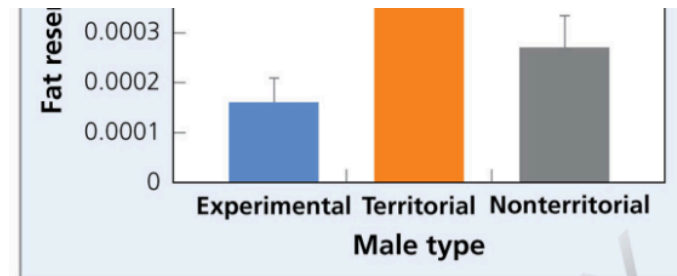
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**FIGURE 11.11.** Fat reserves in male American rubyspot damselflies. Mean (+ SE) fat reserves in grains (1 grain = 0.06 g). Territorial males had higher fat reserves than nonterritorial males. Inset: Territorial male rubyspot damselfly. (Source: [Contreras-Garduño, Canales-Lazcano, & Córdoba-Aguilar 2006](#))

In their second experiment, Contreras-Garduño and colleagues staged territorial fights. They created “intruders” by capturing sexually mature males and tying them to a wooden stick with a thread attached to their thorax, which still allowed them to fly. These males were used to intrude upon a territorial male in the field. The intruders were brought close to the territorial male repeatedly for 20 minutes to simulate a long territorial contest. After the experiment, the fat reserves of the experimental males were measured and compared to those of nonmanipulated territorial males and those of a set of nonterritorial males.

Territorial males who were forced to interact with intruders for 20 minutes had the lowest fat reserves of all three groups (Figure 11.12). The territorial males that were not manipulated had fat reserves that were almost four times higher than those of the experimental males. The researchers concluded that the long staged contests reduced a territorial male’s fat reserves to very low levels, indicating that the aerial displays required for defending a territory are indeed energetically very costly. The study suggests that only males with high energy reserves can hold a territory. As we will continue to see, territory defense is costly. In the next study, we examine how the costs of defense affect territory size in fish.



**FIGURE 11.12.** Male damselfly fat reserves after experimental challenge. Experimentally challenged males (blue) forced to defend their territory had lower mean (+ SE) fat reserves than did nonchallenged territorial males (orange) or nonterritorial males (gray) (units are grains). (Source: [Contreras-Garduño, Canales-Lazcano, & Córdoba-Aguilar 2006](#))

## FEATURED RESEARCH Environmental factors and territory size in parrotfish

Several factors affect the benefits and costs of territory defense (Brown 1964). One of the most important is the density of competitors. As the number of competitors increases, the cost of defense also increases, because there are more potential intruders. An individual can reduce this cost by defending smaller territories, because they involve less area to defend. This leads to the simple prediction that territory size should be negatively correlated with competitor density.

Peter Mumby and Colette Wabnitz tested this prediction by examining territory size and competitor density in the striped parrotfish (*Scarus iseri*) (Figure 11.13) (Mumby & Wabnitz 2002). Parrotfish are sequential hermaphrodites, and individuals exhibit distinct color phases: females and young males are drab-colored, while breeding males display a variety of striking colors. A breeding male defends a territory that encompasses one or more female territories, and the male mates with the females each day (Clifton 1989). Such females are known as a male’s harem because he defends them from rivals.

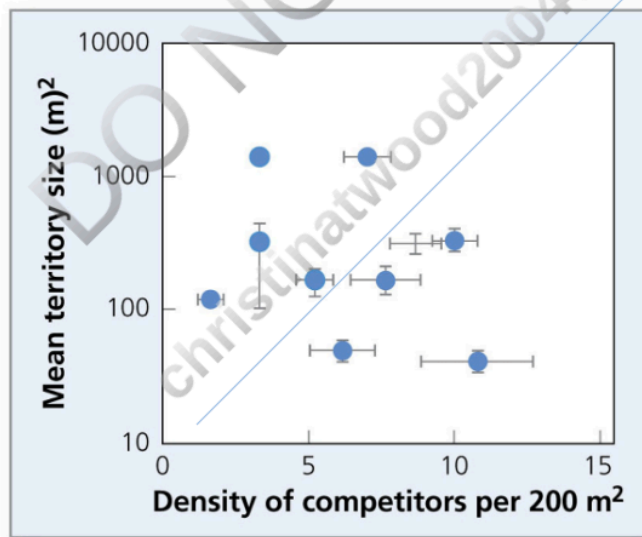




**FIGURE 11.13. Striped parrotfish.** Colorful breeding males defend territories on a reef.

The researchers collected data in Belize at multiple sites that differed in parrotfish density. At each site, they recorded the density of parrotfish along multiple transects. Over a two-month period, they estimated territory size for all breeding males by observing each male's repeated pattern of movement as it patrolled its territory on the reef. The research team recorded all interspecific interactions between conspecifics, which were common at territory boundaries. During territory observations, the researchers also noted the presence of all females within a male's territory.

The density of intra- and interspecific competitors varied from about two to ten individuals per 200 m<sup>2</sup> across sites, and there was a positive correlation between parrotfish density and the number of interspecific interactions at territorial boundaries. Territory size also varied tremendously, ranging from less than 100 m<sup>2</sup> to over 1,000 m<sup>2</sup>. Male territory size declined as conspecific density increased (Figure 11.14), and male harem size also declined with an increase in the density of rivals. In this species, territory size is strongly affected by the density of competitors, as predicted. As the costs of territory defense rise, males apparently reduce the size of their territory, presumably to better defend their harems from rivals.

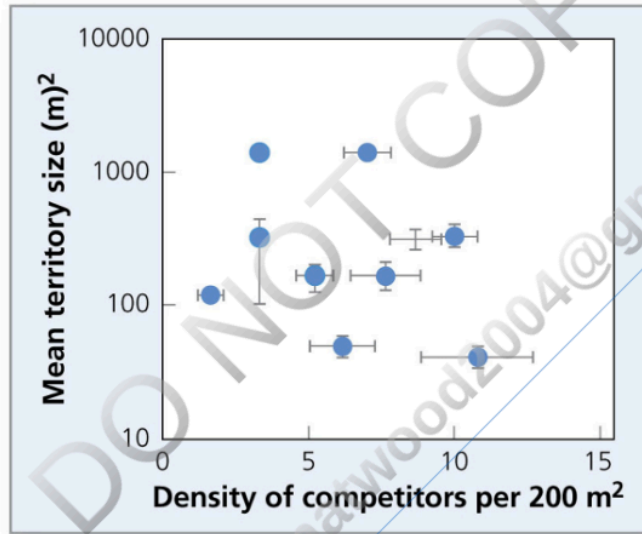


**FIGURE 11.14. Parrotfish territory size.** Mean ( $\pm$  SE) territory size declined with an increasing mean ( $\pm$  SE) density of competitors.

These examples demonstrate that individual condition and environmental factors affect territoriality. The acquisition and defense of a territory or other valuable resource often requires aggressive interactions with rivals. Next, we examine how such aggression is regulated.



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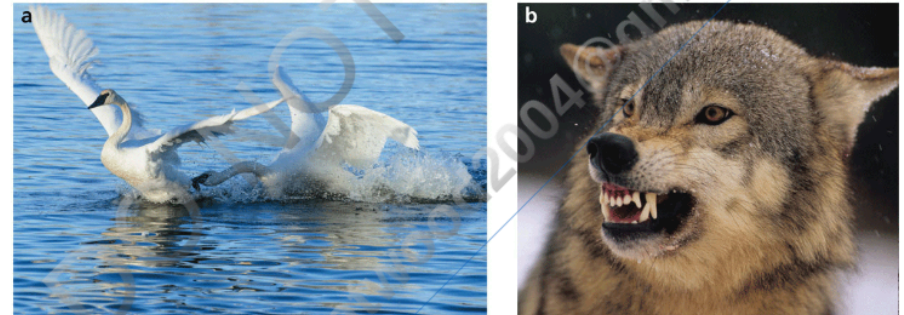
### 11.3 Hormones influence aggression

#### Learning Objectives

After reading this section, you should be able to

- explain the challenge hypothesis,
- explain how a winner effect influences the outcome of aggressive interactions, and
- explain how testosterone and juvenile hormone influence aggression.

Contests over resources involve a variety of aggressive behaviors, including chasing, pushing, wrestling, and fighting, as well as others that indicate the threat of attack, such as particular postures or displays (Figure 11.15). Some species defend territories year-round and thus may aggressively defend their territories regularly, while others defend a territory only during the breeding season. For example, many birds defend territories during summer (the breeding season) but live in large social groups during winter (the nonbreeding season). Therefore, the aggression levels in these species will vary greatly over the course of a year, with high levels at the start of the breeding season and low levels outside the breeding season.

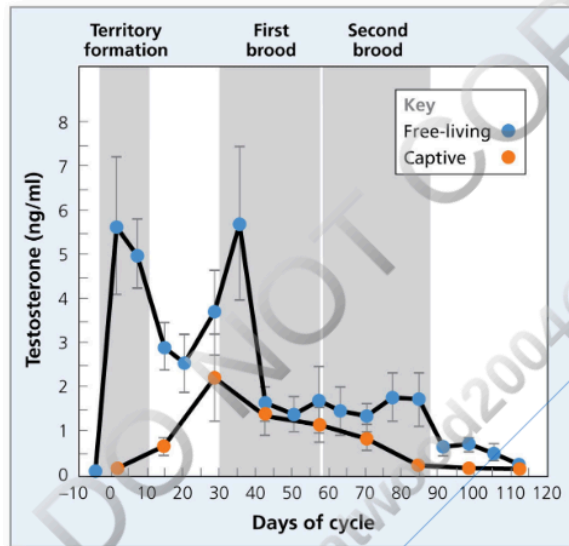


**FIGURE 11.15. Aggression.** (a) A swan chases a rival to defend its territory. (b) Wolves bare their teeth during threat displays.

What regulates aggression? In many vertebrates, variation in aggression is coincident with variation in levels of plasma androgen hormones such as **testosterone**. This steroid hormone is produced in the gonads and is regulated by the hypothalamus and pituitary gland. Androgen hormones have widespread effects on both physiology and behavior. For instance, increased testosterone levels are associated with increases in aggression, sexual behavior, and spermatogenesis. But high testosterone levels are also associated with the suppression of parental care behavior and fat stores, altered immune system function, and increased mortality (Wingfield, Lynn, & Soma 2001). Thus, elevated testosterone levels enhance aggression and fighting ability, but at a cost to other aspects that affect individual fitness. Such counteracting effects on fitness suggest an important role for tight regulation of androgen levels.

In many species that reproduce seasonally, plasma testosterone levels coincide with changes in photoperiod. There is increased production in spring as days grow longer and decreased production in autumn as days become shorter.

is increased production in spring, as days grow longer, and decreased production in autumn, as days become shorter. John Wingfield and colleagues documented such changes in plasma testosterone levels in male song sparrows (*Melospiza melodia*) (Wingfield et al. 1990; Wingfield et al. 2000; Wingfield, Lynn, & Soma 2001). Free-living males displayed very high spikes in testosterone levels in early spring during territory acquisition, as well as a few weeks later when mating, but testosterone levels declined greatly after that (Figure 11.16). Socially isolated captive birds displayed a similar seasonal pattern, but with much lower spikes (Wingfield, Lynn, & Soma 2001). High levels of testosterone (and associated aggression) may facilitate the acquisition of territories early in spring, with a reduction corresponding to the need for males to provide increased levels of parental care once eggs hatch (Chapter 14).



**FIGURE 11.16. Testosterone variation in male song sparrows.** Free-living males (blue circles) had high mean ( $\pm$  SE) plasma testosterone levels during territory formation and reproduction of the first brood. Captive males (orange circles) showed similar patterns of variation over the spring, but with lower levels of testosterone. (Source: Wingfield, Lynn, & Soma 2001)

Why might free-living birds display higher levels of testosterone compared to isolated captives? One possibility is that social interactions also affect testosterone secretion. Wingfield's **challenge hypothesis** states that male-male interactions (over territories, dominance status, or mates) increase plasma testosterone and thus sustain subsequent aggressive behavior (Wingfield, Lynn, & Soma 2001). When males fight over territories and mates, success in a contest can strongly enhance fitness. Enhanced testosterone levels are predicted to increase aggressive behavior and therefore an individual's probability of winning a contest. This can also explain a phenomenon known as the **winner effect**: for many animals, winning an aggressive interaction often enhances the likelihood of winning a subsequent interaction (Hsu, Earley, & Wolf 2006). A combination of the winner effect and the challenge hypothesis, the **winner-challenge effect**, states that winning a challenge increases plasma testosterone levels that

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enhance aggressive behavior and thus the likelihood of winning subsequent interactions (Oyegbile & Marler 2005).

### Video: Song Sparrow singing

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## FEATURED RESEARCH Winner-challenge effect in the California mouse

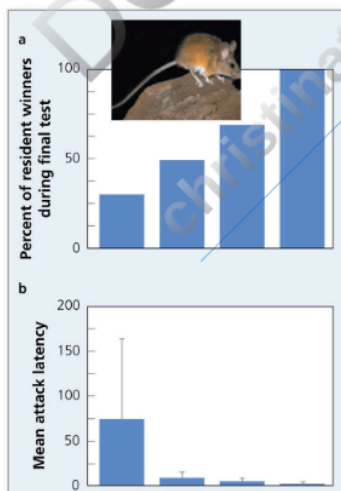
Temitayo Oyegbile and Catherine Marler examined the winner-challenge effect by exploring the links between

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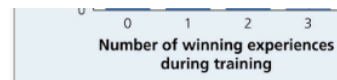
Christina Wood and Catherine Marler examined the winner-challenge effect by exploring the links between testosterone levels, aggressive behavior, and the outcome of contests in the California mouse (*Peromyscus californicus*) (Oyegbile & Marler 2005). California mice aggressively defend their territory year-round, and, like many other species, larger individuals typically win aggressive interactions (Huntingford & Turner 1987).

To test this idea, the research team randomly assigned focal males to one of four training treatments that differed in the number of times (from zero to three) that a male won an interaction with a rival. In a fifth no-interaction control group, males never interacted with a rival. Prior to training, all males were paired with a female for ten days. On Day 11, the pair was placed in a large observation cage that contained a small nest box that allowed the mice to establish residency of the cage. Training interactions were performed on Days 13, 15, and 17 and consisted of either a winning encounter with a rival or simple handling by the experimenters. To create winning encounters, the female was removed and a smaller, mildly sedated male intruder was introduced to the observation cage for ten minutes. On Day 19, the testing phase began. The female was removed, and an unfamiliar and slightly larger male that had previously won an encounter was introduced to the cage. Oyegbile and Marler recorded the resident male's latency to attack, the number of attacks, and the outcome of the contest (winning behaviors included chasing and wrestling; losing behaviors included jumping away, freezing, and retreating). Baseline blood samples were taken from all males before training began and again 45 minutes after the test encounter.

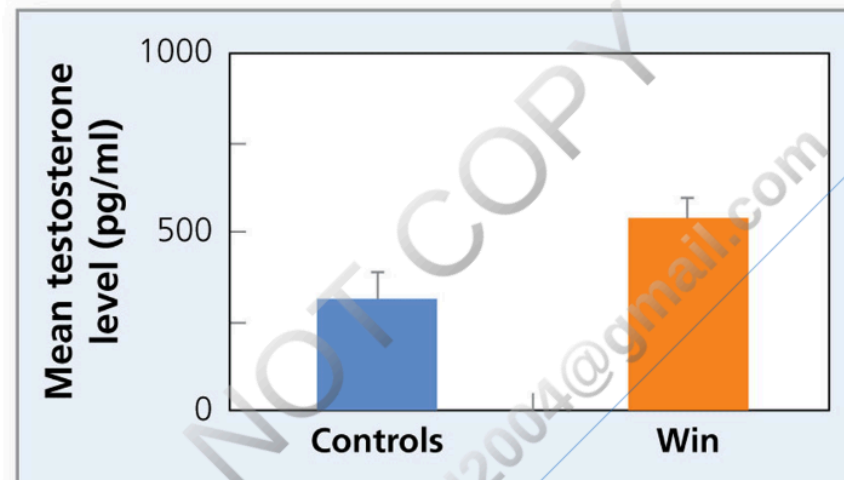
The number of winning encounters a male had in the training phase correlated with an increased likelihood of winning the test encounter. However, the only significant differences were between males with no prior experience and males with three prior winning experiences. Males that won more training-phase encounters also had significantly shorter latency to attack the rival (Figure 11.17). Testosterone levels were higher in mice that had previous winning experiences compared to controls that had none (Figure 11.18). These results support the challenge hypothesis, because variation in plasma testosterone levels correlated with higher levels of aggression and contest outcome. This finding also provides a proximate explanation for the winner effect: winning fights results in elevated plasma testosterone levels, which makes males more aggressive and enhances their likelihood of winning subsequent fights. Together, these results illustrate the winner-challenge effect in mice.



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**FIGURE 11.17. Mouse contest results.** Mice that won more previous contests in training had (a) a higher winning percentage against a larger rival in the final test and (b) a lower mean (+ SE) latency to attack. Inset: California mouse. (Source: Oyegbile & Marler 2005)



**FIGURE 11.18. Testosterone levels in mice.** Mean (+ SE) testosterone levels were higher in males that won fights compared to controls. (Source: Oyegbile & Marler 2005)

## FEATURED RESEARCH Challenge hypothesis and bystanders in fish

Can the challenge hypothesis be extended to bystanders? Does simply observing aggressive interactions affect hormone levels? Rui Oliveira and colleagues examined these questions using the Mozambique tilapia (*Oreochromis mossambicus*) (Oliveira, Lopes, & Carneiro 2001). These cichlid fish are native to East Africa, and males defend territories during the breeding season.

The researchers first kept all fish in isolation for seven days to minimize any effects of previous interactions. Treatment focal male bystanders were then allowed to view two conspecifics interacting. The conspecifics were initially visually separated by an opaque partition and so could not interact. The partition was

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## 11.4 Game theory models explain how the decisions of opponents and resource value affect fighting behavior

### Learning Objectives

After reading this section, you should be able to

- describe the assumptions and predictions of the hawk-dove model,
- identify the resource holding potential of an individual, and
- distinguish self-assessment from mutual assessment game theory aggression models.

Contests over resources involve interactions with others. These contests can be quite complex because individuals often exhibit a variety of aggressive behaviors that differ in intensity. The benefits of aggression are straightforward: the acquisition of a contested resource. But the costs of fighting are more complex because they are affected by the intensity of the aggressive behaviors displayed by both opponents. If an opponent decides to flee, fighting has a low cost. If an opponent decides to fight intensely and is a superior fighter, the decision to fight intensely could be costly, resulting in injury.

For example, male fruit flies commonly fight over food. Fights can be as short as a few seconds or longer than four minutes (Chen et al. 2002) and can include chasing, pushing, tussling (in which opponents tumble over one another), and even boxing—a fight in which opponents rear up on their hind legs and strike each other with their forelimbs (Figure 11.23). The longer the contest lasts, the greater the number of behaviors exhibited and the higher the costs (Chen et al. 2002), but rarely is an individual killed. Why is there so much variation in contest behavior?



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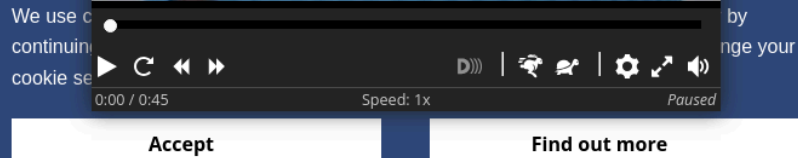
**FIGURE 11.23. Flies boxing.** Fruit flies engage in contests over food.

We can answer this question using **game theory**, a cost-benefit approach used to understand the evolution of behavior when an individual's fitness is affected by how other individuals behave (Chapter 3). Let's see how this works using a very basic game theory model that examines contests between two individuals: the hawk-dove model.

### Video: Fruit flies boxing 1

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### Video: Fruit flies boxing 2

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## The hawk-dove model

[John Maynard Smith and George Price \(1973\)](#) introduced the **hawk-dove model** to examine the behavior of two individuals engaged in a contest over a resource, such as a territory. The winner of the contest obtains a benefit  $B$  that enhances fitness. The loser receives no benefit. In this simple game, both individuals have the same fighting ability and adopt one of two behavioral strategies: hawk or dove. Hawks are always willing to escalate an interaction into an intense, prolonged fight in order to win. In fact, they fight until they are injured (when they give up) or until they win. Losers of these intense fights are injured and pay a cost  $C$ . Doves, on the other hand, back down immediately if their opponent escalates its behavior and so never actually fight or pay the cost  $C$ . When two doves fight, they engage in a short, no-cost display, and each has a 50% chance of winning.

The model allows us to predict the frequencies of these strategies in a population. When  $B < C$ , the model predicts that a population will contain both hawks and doves. At the evolutionary stable strategy (ESS; see [Chapter 3](#)), the frequency of hawks is predicted to be  $B/C$  ([Toolbox 11.1](#)), and, by definition, both hawks and doves have the same fitness at the ESS. Such a population will exhibit tremendous variation in fighting behavior: When two hawks meet, fights will be long and intense. When a hawk interacts with a dove, the contest will be very short, and the individual playing the hawk strategy will always win. Contests between two doves will also be short but will involve only low-cost displays, and so any one individual will win some fights and lose others. This variation is similar to that observed in the real-life contests between animals that Maynard Smith and Price wanted to explain. Interestingly, when  $B > C$ , the model predicts that a population will consist of individuals exhibiting only the hawk strategy, because that situation yields higher fitness than the dove strategy.

### TOOLBOX 11.1

#### The hawk-dove model

John Maynard Smith and George Price introduced the application of game theory to evolutionary biology ([Maynard Smith & Price 1973](#)). They wanted to understand why conflicts between individuals of the same species rarely resulted in death, even when individuals possessed effective weapons such as horns or fangs. Their hawk-dove model examines the outcomes of fights between individuals who can display only two behavioral strategies: hawk or dove. The hawk fights until it wins or is injured. The dove never fights. Maynard Smith and Price assigned benefits and costs to individuals playing these strategies against one another. There are three possible interactions:

##### Hawk versus hawk:

Each player has a probability of 0.5 of winning or losing.

Winners get a benefit  $B$ .

Losers receive no benefits, are temporarily injured, and pay a cost  $C$ .

When hawks play hawks, the average payoff is  $0.5B - 0.5C = 0.5(B - C)$ . In other words, half

When hawks play hawks, the average payoff is  $0.5B - 0.5C = 0.5(B - C)$ . In other words, half the time an individual wins and gets a payoff  $B$ , while half the time the individual loses and pays a cost  $C$ .

#### Dove versus dove:

Each player has a probability of 0.5 of winning.

Winners obtain a benefit  $B$ .

There are no costs, because the players never escalate the conflict and so are never injured.

When doves play doves, the average payoff is  $0.5B$ .

#### Hawk versus dove:

Hawks always win and receive a benefit  $B$ .

Hawks pay no costs, because the dove always retreats.

Doves always lose and get no benefits, but they also pay no costs.

When a hawk plays a dove, the payoff to the hawk is  $B$ , and the payoff to the dove is 0.

Let's look at the benefits and costs to a focal hawk or dove in a matrix. The payoffs in the matrix are read left to right and are based on the opponent's behavior:

	Hawk opponent	Dove opponent
Focal hawk payoff	$0.5(B - C)$	$B$
Focal dove payoff	0	$0.5B$

Maynard Smith and Price assumed that in this game, the cost of losing a contest was greater than the benefit of winning the resource. This means that  $B < C$ .

Given this game, what strategy is the ESS? Let's evaluate some possibilities.

### A Population of all Doves is not an ESS

If all individuals are doves, all interactions are dove versus dove, and so all individuals obtain a fitness of  $0.5B$ . However, if a hawk individual enters this population, or if one of the doves changes its behavior and adopts the hawk strategy, it will receive a reward  $B$  during all encounters with doves and so will have a higher fitness because  $B > 0.5B$ . In a population of all doves, hawks can successfully invade, and so pure dove is not an ESS.

### A Population of all Hawks is not an ESS

In a population of all hawks, each individual receives a payoff of  $0.5(B - C)$ . Because we assume that  $B < C$ , here, individuals actually receive a negative payoff! Remember that they all receive the same negative payoff because all interactions are hawk versus hawk. However, if a dove enters this population, it will lose all contests with hawks but never get injured. The dove's payoff in these encounters will be 0, which is greater than  $0.5(B - C)$  when  $B < C$ . That means

payoff in these encounters will be 0, which is greater than  $0.5(B - C)$  when  $B < C$ . That means that in a population of all hawks, a dove will have the highest fitness—even though the dove can never win a contest. Doves will therefore increase in the population, and so pure hawk is also not an ESS.

### A Population of Hawks and Doves is an ESS

Given that pure dove and pure hawk are not ESSs, is there an ESS for this game? As you might have guessed, the ESS must be a mixture of the two strategies. In a mixed evolutionary stable strategy, a fraction of individuals play each strategy, or else each individual plays a particular strategy in some fraction of the encounters. To solve for the mixed ESS, we need to find the frequency of hawks and doves in the population such that each strategy receives the same fitness. We can solve this mathematically by letting

$p$  = the frequency of hawks in the population

$q$  = the frequency of doves in the population

By definition,  $p + q = 1$ , because all individuals are either a hawk or a dove. Next, we calculate the payoffs for a hawk and a dove based on their frequency in the population. Hawks will encounter hawks a fraction  $p$  of the time, and doves a fraction  $q$  of the time. There are  $p$  hawks in the population, and each time a hawk encounters another hawk, it receives a payoff of  $0.5(B - C)$ . There are  $q$  doves in the population, and each time a hawk encounters a dove, the hawk receives the benefit  $B$ .

The overall payoff to a hawk will then be:

$$p[0.5(B - C)] + qB$$

By the same reasoning, the overall payoff to a dove will be:

$$p(0) + q(0.5B)$$

Now all we need to do is to set the payoff to a hawk equal to the payoff to a dove:

$$p[0.5(B - C)] + qB = p(0) + q(0.5B)$$

A little algebra gives us:

$$p = B/C$$

Therefore, in a population at the ESS, the frequency of hawks will be  $B/C$ .

The hawk-dove model introduced game theory to animal behavior and has also been used extensively in economics, political science, and even cancer research (e.g., [Hanauske et al. 2009](#); [McEvoy 2009](#)).

The introduction of the hawk-dove model to animal behavior research was an important conceptual advance in our understanding of fighting behavior for several reasons. First, it showed how individual selection (as opposed to group selection) could explain why individuals did not fight to the death when competing over resources. Second, it predicted variation in fighting behavior in a population depending on the benefits and costs involved in the contest. And third, it focused empirical effort on understanding the benefits and costs of fighting behavior.

While the model has important heuristic value, it was likely never intended to explain in detail the fighting



behavior of actual animals (Fawcett & Mowles 2013; Kokko 2013). Recall that one of its assumptions is that animals have identical fighting ability, an unlikely occurrence in nature. Instead, individuals will often differ greatly in their fighting ability or **resource holding potential (RHP)** (Parker 1974). Differences in fighting ability will be influenced by an individual's size, condition (health), and endurance (energetic stores), among other factors. Many studies have shown that RHP affects the outcome of contests: the greater the asymmetry in RHP, the more likely that the individual with greater RHP will win a contest (e.g., Kemp & Wiklund 2004; Briffa & Sneddon 2007).

The hawk-dove model also has little to say about variation in contest duration. The duration of actual contests can be quite variable and is often affected by the value of the contested resource. For instance, males often engage in contests with other males for access to a female (or group of females). This is particularly common in amphibians, in which reproduction often involves amplexus, a behavior in which a male grasps a female and holds her for up to several hours before she releases eggs he will fertilize. During amplexus, rival males will attempt to displace an amplexed male by wrestling with him. How much effort should an intruding male invest in these contests?

## FEATURED RESEARCH Wrestling behavior in red-spotted newts

Paul Verrell examined wrestling behavior in red-spotted newts (*Notophthalmus viridescens*) (Verrell 1986). These small salamanders (< 125 mm long) are common in eastern North America (Figure 11.24). In amphibians, female fecundity, as measured by number of oocytes, typically increases with body size, indicating that larger females should be more valuable to a male. Verrell first verified that larger females had a higher resource value by observing that larger females laid significantly more eggs than did smaller females.



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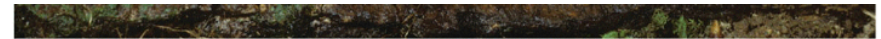


FIGURE 11.24. Red-spotted newts. Males wrestle with rivals for access to mates.

With this information, Verrell predicted that the fighting intensity of males should increase with the size of the contested female. To test this prediction, he staged encounters between size-matched males in a large aquarium. In each trial, one female, whose body size ranged from 43 mm to 51 mm, was placed in the aquarium along with two males. One of the males quickly initiated amplexus, and in 33 trials, the rival male began a wrestling contest with the amplexed male. The wrestling bout ended either when the rival left the amplexed pair or when he successfully detached the amplexed male from the female.

The total duration of the wrestling contest increased with the size of the female, as predicted (Figure 11.25), and the intruder did displace the amplexed male in four of the trials. These data illustrate how the value of a contested resource affects the intensity of aggressive behavior. Males spent more time wrestling over large females than they did over small females, as one might expect, given that larger females lay more eggs.

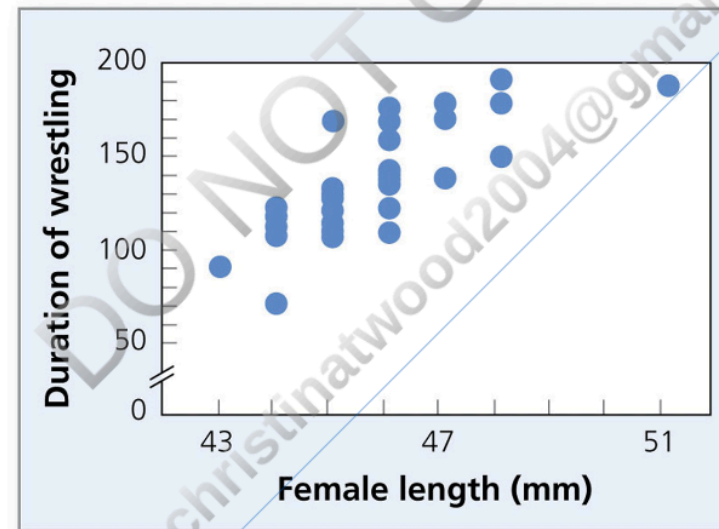


FIGURE 11.25. Duration of wrestling in male red-spotted newts. The duration of wrestling increased with the size of the female that was amplexed. (Source: Verrell 1986)

## Game theory assessment models

Another aspect of contests not fully incorporated into the hawk-dove model is that contests typically begin with opponents exhibiting display behaviors, often with no physical contact. For example, many birds and crickets will

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begin a contest by singing, fiddler crabs will start a contest by waving their claws, and lizards will begin a contest with head-bob or push-up displays. After some time, contests such as these may escalate as more energetically costly behaviors are used, often leading to physical contact.

One classic example of such a contest sequence of escalated behavior involves fights between male red deer (*Cervus elaphus*). Aggressive interactions during the breeding season typically begin with males engaging in a roaring contest (Clutton-Brock & Albon 1979). As the contest continues, males will subsequently engage in a parallel walk in which they stride next to each other for up to 30 minutes. Finally, if the contest is still not decided, individuals will lock antlers and physically push against each other (Figure 11.26). At any time during this process, one individual may decide to abandon the fight, and so we see tremendous variation in contest duration, ranging from a few minutes to over one hour (Clutton-Brock & Albon 1979).



**FIGURE 11.26. Red deer contest.** Males lock antlers and push against one another during a contest.

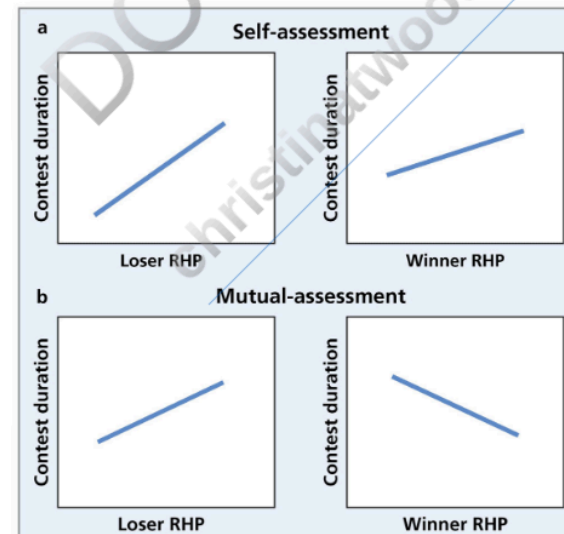
These observations prompted the development of more sophisticated game theory models that assume that a contest entails time and energy costs, and that these costs increase with the duration of the contest. The models also assume some form of assessment by individuals of the conditions in which the contest takes place. Such conditions can include the perceived value of the resource as well as the relative RHP of the contestants. Unlike the hawk-dove model, these more advanced game theory models predict the amount of effort an individual should allocate to a particular contest and so predict variation in contest duration.

Two basic types of game theory assessment models exist. **Self-assessment game theory models** (e.g., Mesterton-Gibbons, Marden, & Dugatkin 1996; Payne & Pagel 1996) assume each individual assesses the value of the resource and engages in the contest until the individual reaches a cost threshold beyond which it is unwilling to

resource and engages in the contest until the individual reaches a cost threshold beyond which it is unwilling to continue, and so gives up. An individual's cost threshold will be based on assessments of its RHP and the value of the resource. A contest will continue until the first individual (the loser) reaches its cost threshold and abandons the fight. These models predict that contests will always be won by the individual with the higher RHP, and that contest duration will increase as the loser's RHP increases and as the value of the resource increases.

**Mutual-assessment game theory models**, like the sequential assessment model (Enquist & Leimer 1983), assume that each individual assesses the relative cost threshold of itself and its opponent and continues the contest until an individual assesses that it is unlikely to win the contest (because it has a lower cost threshold). In essence, these models envision that each individual assesses its RHP and that of its opponent (its relative fighting ability) and decides to give up when it estimates that it has the lower RHP (and so will eventually lose the contest). The models assume that each contestant is unsure of its opponent's RHP and so acquires information about its opponent during the contest. These models also predict that contest duration will increase with the value of the contested resource.

How can we distinguish these models of assessment? Let's examine the predictions they make regarding the duration of a contest and the RHP of winners and losers (Taylor & Elwood 2003). Imagine that in any population, you score the RHP of all individuals from lowest to highest. Now imagine recording the duration of contests between random pairs of individuals and assume that the individual with the higher RHP always wins. Self-assessment models predict that there should be a strong positive correlation between the losers' RHP and contest duration: losers with higher RHP will engage in longer contests before they lose (Figure 11.27). Mutual-assessment models also predict a positive relationship between loser RHP and duration, but for different reasons. In these models, a loser with a low RHP will often lose to a winner with a high RHP, making assessment of the relative difference easy and the contest short. As loser RHP increases, the difference in RHP between the loser and the winner declines, making assessment more difficult and contests last longer.





**FIGURE 11.27. Assessment model predictions.** (a) Self-assessment models predict that contest duration increases with both loser and winner RHP. (b) Mutual-assessment models predict that contest duration increases with loser RHP but declines with winner RHP. (Source: [Gammell & Hardy 2003](#))

However, self-assessment and mutual-assessment models make distinctive predictions regarding contest duration and winner RHP. Self-assessment models predict a positive relationship between contest duration and winner RHP because longer contests (i.e., higher loser RHP values) require a higher winner RHP to ensure that the winner wins. Mutual-assessment models, however, predict a negative relationship between winner RHP and contest duration. Winners with low RHP will have beaten losers with similarly low RHP, making assessment difficult and contest duration long. But winners with high RHP will often be matched with low-RHP losers, making assessment easier and contest duration shorter ([Taylor & Elwood 2003](#)).

A second prediction can be made for fights between RHP-matched individuals. The self-assessment models predict that for individuals with matched RHP, loser RHP will determine contest duration. Therefore, we will see short contests between two low-RHP individuals and much longer contests between two high-RHP individuals: there will be a positive correlation between mean RHP of rivals and contest duration. In contrast, mutual-assessment models predict no effect of mean RHP: all contests between RHP-matched individuals should be long and similar in duration.

Let's examine one test of these predictions for fights involving male fiddler crabs.

## FEATURED RESEARCH Fiddler crab contests over burrows

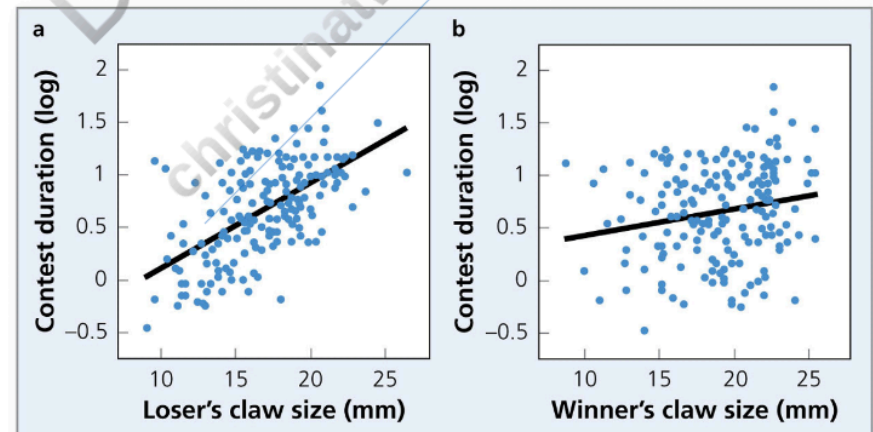
Fiddler crabs aggressively defend burrows they create in mudflats. Burrows provide a safe refuge, and females select mates based partly on their burrow characteristics; consequently, possession of a burrow strongly affects male fitness. Leslie Morrell, Patricia Blackwell, and Neil Metcalfe studied fights between males in a population of *Uca mjoebergi* fiddler crabs in Australia ([Morrell, Blackwell, & Metcalfe 2005](#)). They captured burrow-holding males and released them far away from their burrow. These "intruder" males quickly engaged in contests with burrow-holding residents. Contests began with claw touching and could escalate to pushing and grappling with the major claw ([Figure 11.28](#)). The research team recorded the duration and winner of 173 contests. The winner was the occupant of the contested burrow at the end of the contest. They also measured the size of each individual (major claw length) to characterize its RHP.



**FIGURE 11.28. Fiddler crab contest.** Fiddler crabs use their major claws during a contest.

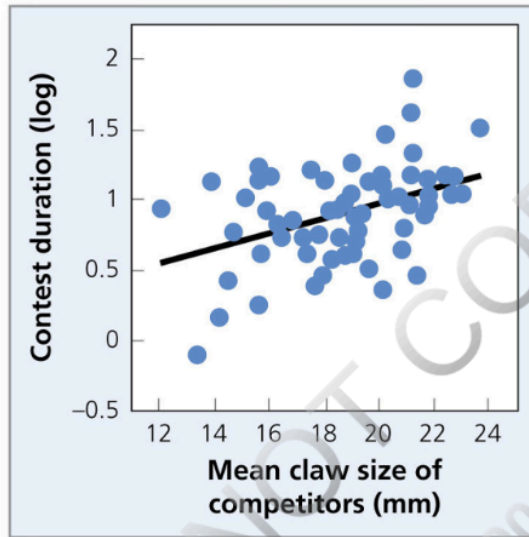
Intruders won one-third of the contests. Both claw size (RHP) and status (burrow-holder or intruder) influenced the outcome of fights: the individual with the larger major claw won more contests, and burrow-holders tended to beat intruders when individuals were similar in size. Contests averaged seven seconds in duration, but some lasted over 60 seconds. There was a strong positive correlation between contest duration and loser claw size and a weaker positive correlation between contest duration and winner claw size ([Figure 11.29](#)). For size-matched contests, the researchers found a positive correlation between mean combatant claw size and contest duration ([Figure 11.30](#)). These data are consistent with the predictions of self-assessment models, as contest duration was positively related to both loser RHP (claw size) and winner RHP. Furthermore, for size-matched fights, contest duration increased with size.

Game theory models have been instrumental in providing unique insight into understanding the evolution of, and variation in, fighting across species. These models are also being increasingly used in agricultural settings to manage animal aggression ([Applying the Concepts 11.3](#)).





**FIGURE 11.29. Fiddler crab contest duration.** Contest duration was positively correlated with (a) loser and (b) winner RHP, as measured by major claw size.



**FIGURE 11.30. Contest duration for size-matched crabs.** Contest duration increased with the mean size of the competitors.

### APPLYING THE CONCEPTS 11.3

#### Reducing duration and intensity of piglet fights

In the agricultural production of domestic pigs (*Sus scrofa domesticus*), many litters are born simultaneously. The piglets in a litter are housed together with their mother but are kept physically and visually isolated from other litters. After several weeks, piglets from different litters are mixed together, which results in aggressive fights. These fights are often intense and can result in injury, making them a major welfare and production issue. Farmers have tried to reduce fighting with drugs and masking odors, but they have had little success.

Per Jensen and Jenny Yngvesson applied game theory models to piglet fights (Jensen & Yngvesson 1998). Fights often begin with a low-intensity nosing phase, in which two individuals walk together and exchange nose contact. After a period of time, fights can escalate to a biting phase, in which individuals push and bite each other until the loser retreats. Jensen and Yngvesson reasoned that if opponents rely on fights to learn each other's relative fighting ability, as assumed by mutual-assessment models, allowing interactions of individuals before a contest should produce shorter and lower-intensity fights.

### CHAPTER SUMMARY AND BEYOND

Animals select habitats in which to live and reproduce based on the resources those habitats contain and the presence of others. When habitats exhibit negative density-dependent fitness and movement is cost-free, individuals distribute themselves among habitat patches in an ideal free distribution. In this pattern, the number of individuals in a habitat is proportional to habitat quality, and all individuals obtain the same fitness. Additional work has examined how distributions change when individuals are not free to select a habitat because of the behavior of dominant individuals (Murray, Mane, & Pusey 2007; Purchase & Hutchings 2008). In some cases, fitness does not decline as density increases, and we then observe conspecific attraction, either because of Allee effects or because of conspecific cueing. Ongoing work has investigated the relative importance and consequences of these mechanisms (Donahue 2006; Gil et al. 2018).

Once a habitat is selected, individuals often defend a territory to secure the resources it contains. Territory defense is costly and so only individuals with high energy reserves can defend territories successfully. Understanding the costs of defense for individuals is an active area of research (Müller & Manser 2007; Baird & Curtis 2010). Territory defense and contests over resources require aggressive interactions that are regulated by androgen hormones such as testosterone. Androgen hormone levels are often elevated by social stimulation, as articulated in the challenge hypothesis. Hirschenhauser and Oliveira (2006) have reviewed empirical studies of the challenge hypothesis in relation to vertebrates, while Scott (2006) has extended the hypothesis to insects. Other work has examined how these hormones mediate winner effects (Gleason et al. 2009; Oliveira, Silva, & Canário 2009).

Animals exhibit much variation in fighting behavior that can be understood by game theory models, which explain how behavior evolves when fitness depends on how others behave. Game theory models have successfully been used to understand the fighting behavior of many taxa (Arnott & Elwood 2008), predicting that fighting behavior will be affected by resource holding potential (fighting ability) and the value of the contested resource. Additional work has been devoted to understanding how individuals assess their relative fighting ability during a contest (Elias et al. 2008; Hsu et al. 2008; Reddon et al. 2011; Fawcett & Mowles 2013; Elwood & Arnott 2013; Pinto, Palaoro, & Peixoto 2019).

## Chapter Summary and Beyond

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## CHAPTER REVIEW

### 11.1 Resource availability and the presence of others can influence habitat selection

- The ideal free model predicts the relative number of individuals in habitat patches based on patch quality; all individuals obtain equal fitness.
- Guppies exhibit an ideal free distribution when exploiting food patches.
- Cuckoos assess habitat quality based on gypsy moth abundance.
- Some individuals exhibit conspecific attraction when selecting a habitat.

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### 11.2 Individual condition and environmental factors affect territoriality

- Individuals can benefit from Allee effects by settling near others.
- The presence of another individual can serve as an indicator of habitat quality, a phenomenon called conspecific cueing.

- Territories are defended from rivals, home ranges are not.
- Territory defense is costly.
- Only individuals in good condition can successfully defend a territory.
- Territory defense costs affect the size of a territory.

### 11.3 Hormones influence aggression

- In vertebrates, androgen hormones such as testosterone influence aggressive behavior.
- Social interactions affect testosterone secretion: winning a challenge increases plasma testosterone levels, which enhance aggressive behavior.
- In invertebrates, juvenile hormones influence aggressive behavior.

### 11.4 Game theory models explain how the decisions of opponents and resource value affect fighting behavior

- The hawk-dove game theory model predicts the frequency of different fighting strategies in a population.
- The value of a contested resource influences aggressive behavior.
- Assessment game theory models explain why individuals often initially exhibit display behaviors in an aggressive contest.
- Self-assessment models assume individuals only assess their own fighting ability.
- Fiddler crab fighting behavior is consistent with the predictions of self-assessment models.
- Mutual-assessment models assume individuals assess the fighting ability of their opponent relative to their own ability.

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## CHAPTER 10

# Dispersal and Migration

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 10.1 [Dispersal reduces resource competition and inbreeding](#)
- 10.2 [Reproductive success and public information affect breeding dispersal behavior](#)
- 10.3 [Individuals migrate in response to changes in the environment](#)
- 10.4 [Environmental cues and compass systems are used for orientation when migrating](#)
- 10.5 [Bicoordinate navigation allows individuals to identify their location relative to a goal](#)

### Features

- |                        |   |
|------------------------|---|
| Scientific Process     | 10.1 <a href="#">Breeding dispersal in dragonflies</a>                                      |
|                        | 10.2 <a href="#">The role of the antennae in the monarch butterfly sun compass</a>          |
| Applying the Concepts  | 10.1 <a href="#">Bird migration and global climate change</a>                               |
|                        | 10.2 <a href="#">Citizen scientists track fall migration flyways of monarch butterflies</a> |
|                        | 10.3 <a href="#">Human magnetic orientation</a>   |
| Toolbox                | 10.1 <a href="#">Emlen funnels</a>  |
| Quantitative Reasoning | 10.1 <a href="#">Dispersing cane toads</a>  |

One of our favorite excuses for heading outdoors is bird watching, and Arizona has a wonderful diversity of bird species—one of the greatest in the United States. One day, while in graduate school, we were birding in an arid grassland habitat south of Tucson. Like many birders, we keep track of the number of species seen in a day, a year, or a lifetime, and we were hoping to spot a Cassin's sparrow (*Aimophila cassinii*) to add to our list.

or a jaeger, and we were hoping to spot a Cassin's sparrow (*Aimophila cassinii*) to add to our list.

Suddenly, a rather large bird flew directly overhead, maybe 10 m above us ([Figure 10.1](#)). It did not look like any bird we had ever seen before. As we observed the bird carefully we noted a distinct tail: the center tail feathers projected beyond the rest of the tail. This is a characteristic of jaegers, or skuas, as they are called outside of the United States. However, jaegers are pelagic, or open-ocean, birds—hardly the kind found in the middle of Arizona. But they do migrate thousands of kilometers between Alaska, where they breed, and their wintering area in the southern Atlantic. If this was a jaeger, it was terribly off course! We made careful notes of our observations and then reviewed them with our bird guide to determine what species we had just seen. We determined that it was a juvenile long-tailed jaeger. We headed back to school to report our exciting bird sighting, only to find that other birders and experts didn't believe us.



**FIGURE 10.1.** Jaeger. Long-tailed jaeger, a bird that lives in an open-ocean habitat.

About a week later, the curator of the University of Arizona's bird museum called us to see what had just been brought in—a juvenile long-tailed jaeger (*Stercorarius longicaudus*). It had been found dead along a road only a few kilometers from where we had spotted our bird and had probably died from stress. Our identification was vindicated. In fact, our jaeger spotting was not the first in the state. A search of museum records revealed that several jaegers had been observed in Arizona over the past 100 years. All were likely lost, blown off course in a storm, or ill. Migrating is serious business, and not all animals make it.

In this chapter, we examine the how and why of animal movements, ranging from short-distance, one-way dispersal movements to round-trip annual migrations of thousands of kilometers. We discuss the mechanisms that allow animals to make these trips, as well as the benefits of such movements.

### Video: Long-tailed jaeger natural history

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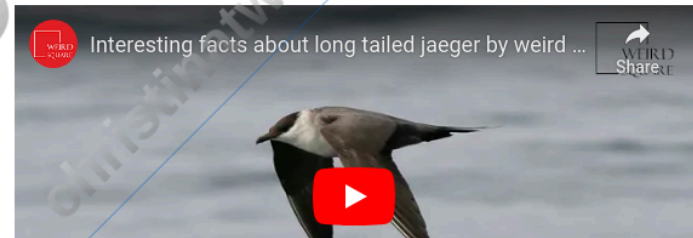
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## 10.1 Dispersal reduces resource competition and inbreeding

### Learning Objectives

After reading this section, you should be able to

- distinguish between the competition and inbreeding avoidance hypotheses and
- describe empirical support for each.

Many animals exhibit **dispersal**, a relatively short-distance, one-way movement away from a site. For dispersal behavior to evolve, the fitness benefit of moving to a new location must exceed the cost. One cost of dispersal involves the time and energy required to move; another is enhanced predation risk while moving through an unfamiliar area. But there is also an important benefit of moving: the new location might result in higher fitness relative to the current site. Locations can differ greatly in their availability of resources and breeding opportunities. As such, the current site might be of low quality as a result of intense competition for resources relative to other locations. Competition for resources is density dependent: it increases with the number of competitors. The competition hypothesis states that dispersal reduces competition for resources.

To test this hypothesis, researchers have manipulated both the density of individuals and the amount of food to which individuals have access, leading to two predictions:

- Prediction 1:** If two sites have identical amounts of food but differ in their density of individuals, we can expect higher levels of dispersal behavior in the high-density sites.
- Prediction 2:** If two sites have the same density of individuals but differ in their quantity of food, we can expect higher levels of dispersal behavior in the site with less food.

Studies have tested each prediction using a variety of taxa, as we see in the next two case studies.

### FEATURED RESEARCH Density-dependent dispersal in earthworms

Earthworms live and feed in and on soil and play an important role in soil and ecosystem functioning. They improve soil fertility by breaking down organic matter and converting it into a rich humus, excreting concentrated nutrients in a form that is accessible for plants. As such, their burrowing movements help to enhance soil structure, but little is known about their mobility and dispersal behavior.

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structure, but little is known about their mobility and dispersal behavior.

Jérôme Mathieu and his colleagues examined whether the density of conspecifics affects dispersal in the earthworm (*Aporrectodea icterica*) (Mathieu et al. 2010). They tested the prediction that greater dispersal behavior would be associated with higher conspecific densities by creating three experimental treatments that differed in the number of earthworms placed into one end of an arena: 10, 20, or 30. Each arena was 1.0 m × 0.18 m long and divided into three equal-sized regions that varied in habitat type. Each end contained “suitable” soil for earthworms, while the center region contained “unsuitable” soil that earthworms tend to avoid. Over the course of one week, the research team recorded the percentage of individuals that had dispersed to the other end of the arena. The experimental design allowed researchers to classify such movements as dispersal rather than simple random movements because individuals had to move over unsuitable habitat.

The treatments did affect dispersal behavior, as a greater fraction of individuals dispersed in the highest-density treatments. For the two lower-density treatments, less than half of the individuals dispersed; in contrast, 69% of individuals dispersed in the highest-density treatment.

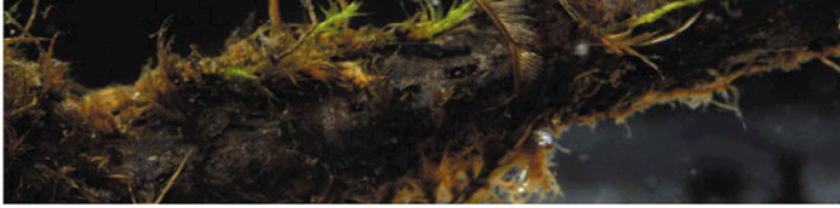
The density of conspecifics in a habitat and the resulting competition for resources affected the earthworms' dispersal behavior. Although these results support the competition hypothesis, they do rely on the common assumption that high density corresponds to intense competition, which drives dispersal behavior. Mathieu and colleagues examined the competition hypothesis by manipulating the density of conspecifics. Another approach is to vary the density of food, as we see next.

### FEATURED RESEARCH Food-related dispersal in water boatmen

If animals disperse from one site because of high competition, one straightforward test of the competition hypothesis is to examine how dispersal behavior is affected by resource level. Josie Simonis (2013) examined how the density of prey affected dispersal behavior of water boatmen (*Trichocorixa verticalis*). Water boatmen are small (2.5 mm–15 mm long) aquatic invertebrate predators that live in freshwater pools and feed on herbivorous aquatic invertebrates (Figure 10.2). Adult water boatmen can fly to disperse from one pool to another.



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**FIGURE 10.2. Water boatman.** These predators disperse from one pool to another in search of prey.

Simonis created 40 artificial pools (20 L in size) that differed in the density of prey, ranging from 0 to 100 water fleas (*Moina macrocarpa*), small crustaceans, per liter. Each day, five experimental pools were established, separated by at least 5 m, with ten adult water boatmen predators in each pool. Each pool contained a different density of prey and was monitored over a 24-hour period to determine the number of water boatmen that had dispersed.

The proportion of predators dispersing away from a pool ranged from 0% to 60%. There was a significant negative effect of prey density on predator dispersal: predators were more likely to disperse from low prey density pools (Figure 10.3). These results are consistent with the hypothesis that competition

On additional factor influences dispersal; adults often exhibit breeding dispersal behavior when they move from one breeding site to another. Hypotheses to explain these movements typically do not involve competition or inbreeding avoidance. Instead, they propose that individuals are attempting to move to a higher-quality breeding site, as we see next.

#### Video: Great tits nestbox

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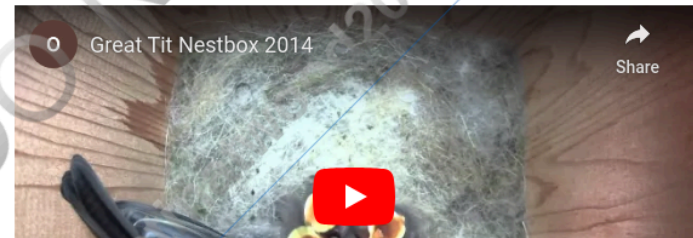
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## 10.2 Reproductive success and public information

## affect breeding dispersal behavior

### Learning Objectives

After reading this section, you should be able to

- differentiate between natal and breeding dispersal,
- predict the win-stay lose-shift dispersal strategy pattern based on reproductive success, and
- describe how public information can affect breeding dispersal behavior.

For many species, a major factor that affects fitness is the ability of parents to raise young successfully. Breeding habitats differ in quality with respect to reproductive success because they differ in food abundance, predators, diseases, and so forth. Animals that settle and breed in a high-quality habitat will tend to have higher fitness than those that settle in a poor-quality habitat. However, it may be difficult for an individual to assess the quality of a habitat accurately, which could result in low reproductive success. Individuals experiencing low reproductive success in a habitat may exhibit **breeding dispersal**—movement to a new breeding site, presumably in search of a higher-quality habitat that will enhance their fitness.

Numerous studies have found a strong relationship between reproductive success and breeding dispersal behavior: individuals that are unsuccessful in a breeding attempt typically disperse to a new site for subsequent breeding attempts (Switzer 1993). In contrast, those that are successful in breeding typically do not disperse: they rebreed at the same site, a pattern known as **site fidelity**. This pattern holds both for individuals that breed seasonally, such as birds in temperate or boreal habitats, and for those that reproduce each day, such as insects. Let's look at one example that illustrates this pattern.

### FEATURED RESEARCH Reproductive success and breeding dispersal in dragonflies

Paul Switzer experimentally examined the breeding dispersal behavior of male eastern amberwing dragonflies (*Perithemis tenera*) on a pond in Kansas (Switzer 1997). Male eastern amberwing dragonflies defend small sites for oviposition (egg laying) that consist of vegetation or sticks rising above the surface of a pond. When a male spots a female, he leads her back to the oviposition site and courts her. If the female finds the site acceptable, she uses it to lay a clutch of eggs, which the male fertilizes. Males defend one site per day and may mate with several females in a day. Males leave the pond at night for the safety of dense vegetation and return the next day to select an oviposition site. They may exhibit site fidelity (by selecting the same site) or breeding dispersal (by moving to a new site) (Scientific Process 10.1).

Video: Eastern amberwing dragonfly

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### Video: Eastern amberwing dragonfly

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Video: Eastern amberwing dragonfly



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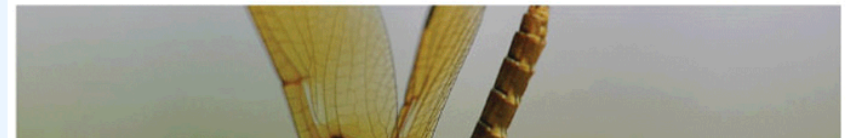
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### SCIENTIFIC PROCESS 10.1

#### Breeding dispersal in dragonflies



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Research Question: *What factors affect breeding dispersal in dragonflies?*

### Hypothesis:

Dragonfly dispersal behavior is affected by their reproductive success.

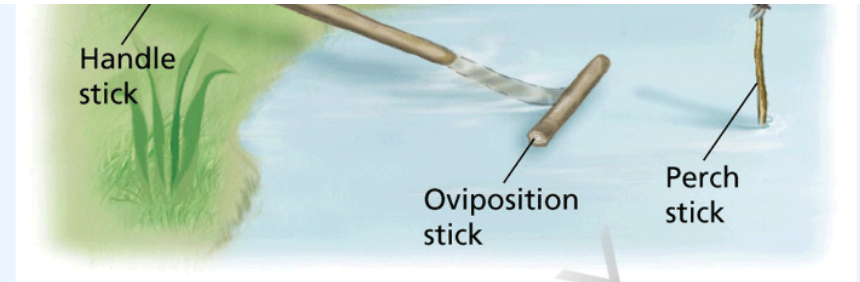
### Prediction:

Dragonflies will remain in the same territory if they have high mating success and will disperse to a new territory if they have low mating success.

### Methods:

The researcher:

- Created 20 breeding territories on a pond using sticks
- Reduced mating success in ten territories (treatment) and kept it high in others (controls)
- Recorded the number of matings for each male and whether he returned to the same territory or dispersed to a different territory on Day 2



**FIGURE 1. Experimental setup.** Experimental setup showing the sticks used to manipulate the oviposition site. (Source: [Switzer 1997](#))

### Results:

Control males had higher mating success than treatment males. All control males returned to their oviposition site, whereas only 50% of treatment males returned to their oviposition site.

### Conclusions:

Mating success affects breeding dispersal: individuals use a win-stay lose-shift strategy when making dispersal decisions.

### Evaluate

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Develop a hypothesis to explain why some of the treatment males that obtained no matings returned to the same site on Day 2.

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To examine how a male's reproductive success affects his dispersal behavior, Switzer created artificial oviposition sites consisting of two sticks joined together. The longer stick served as a handle to allow for manipulation of the site. Males were captured and marked on the forewing for visual identification and then released. On the first day of an experimental trial, two males were selected while defending oviposition sticks on the pond. The treatment male was prevented from mating all day, whereas the control male was allowed to mate with females. To prevent a male from mating, Switzer simply lowered the oviposition stick under the water whenever the treatment male had attracted a potential mate to his territory. With the oviposition site submerged, the female would quickly abandon the male. When she left, Switzer would return the stick to its original position above the water, which allowed the male to continue to defend the site. To control for this manipulation, Switzer also submerged the control male's oviposition stick when he was on his territory, but only when females were not present. Thus, both males had their sites submerged a similar number of times. Switzer recorded the number of matings and the dispersal decisions of each male by locating them on the pond the following day.

Switzer found that control males mated an average of 6.5 times on the first day, but treatment males never mated successfully. On the following day, all control males reused the same site—that is, all exhibited site fidelity. In contrast, half of the treatment males dispersed to a new site on the following day. On average, the treatment males moved 22 m between Day 1 and Day 2, while control males did not move at all. These results clearly demonstrate that an individual's reproductive success affects its decision to disperse to a new breeding site.

The behavioral pattern exhibited by Switzer's dragonflies, and by many other species as well, is known as a **win-stay lose-shift dispersal** strategy. Here, *win* means high reproductive success, while *lose* means a reproductive failure; *stay* and *shift* refer to the dispersal decision. We can explain this behavioral pattern by assuming that breeding sites vary in quality and that the quality of a site is consistent between breeding attempts. That is, we assume that (1) in poor sites, reproductive success is low, while in high-quality sites, reproductive success is high; and (2) a site that is high quality currently is likely to be a high-quality site in the future too. Under these assumptions, the win-stay lose-shift strategy for breeding dispersal makes sense.

So far, we have assumed that the win-stay lose-shift dispersal decision is based on an individual's assessment of breeding patch or site quality. This assessment, in turn, is based solely on the individual's reproductive success in the patch. Thierry Boulinier and Etienne Danchin reasoned that it might be even better for individuals to gather information about the reproductive success of conspecifics breeding in the same patch (Boulinier & Danchin 1997). Using a model, they demonstrated that patch-wide reproductive success of conspecifics provides more

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accurate information about the quality of the patch than does individual success. They also showed that using such information for dispersal decisions results in higher fitness for an individual compared to relying only on its own experience (Boulinier & Danchin 1997; Doligez et al. 2003). Information about the quality of a resource based on the performance or behavior of others is known as public information (Valone 1989). Over the past decade, several studies have shown that animals use public information to improve their estimates of the quality of mates, food patches, and breeding patches (e.g., Doligez, Danchin, & Clobert 2002; Aparicio, Bonal, & Muñoz 2007; Valone 2007). Let's examine one study showing how public information affects the breeding dispersal decisions of birds.

## FEATURED RESEARCH Public information and breeding dispersal in kittiwakes

Black-legged kittiwakes (*Rissa tridactyla*) are gulls that nest in large colonies on sea cliffs in northern Europe (Figure 10.6). The rocky habitat often creates subcolonies, or breeding patches, of just a few dozen individuals, aggregated close together and widely separated from other patches. Kittiwakes breed once a year, and previous work suggested that individuals use the win-stay lose-shift strategy when making breeding dispersal decisions from one year to the next (Danchin, Boulinier, & Massot 1998).



**FIGURE 10.6.** Kittiwake research. (a) Kittiwakes nest in rock cliff colonies. Note the colored leg bands that researchers use to identify individuals. (b) A researcher examines an experimental bird.

Boulinier and colleagues hypothesized that patch-wide reproductive success in subcolonies might also affect

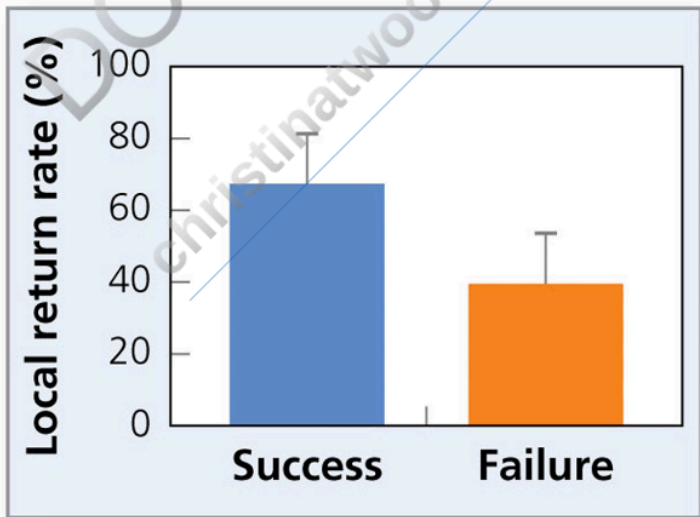
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abandon it in favor of a new site the following year—that is, it should exhibit breeding dispersal. However, if a failed breeder uses patch-wide reproductive success to assess patch quality, and if it is surrounded by many individuals that breed successfully, it should estimate that the patch is of high quality and so should not abandon it the next year—that is, the individual should exhibit site fidelity.

To test these predictions, Boulinier and colleagues uniquely marked focal birds with color bands in 18 breeding patches. These patches were arranged in nine matched pairs, based on size and proximity to one another. One patch of each pair was the treatment, and the other served as the control. In the treatment patches, all birds, including the focal individual, had their eggs removed 25 days after the first egg was laid and every sixth day after that; thus, all birds in the treatment patch experienced a reproductive failure. In the control patches, the focal bird had its eggs removed at the same time as the treatment birds, but none of the other birds' eggs were manipulated, and so they experienced high levels of reproductive success. The research team observed the behavior of focal birds over two years to determine whether they exhibited breeding dispersal or site fidelity.

The manipulation created a large difference in the patch-wide reproductive success of the paired patches. No bird in the treatment patches successfully raised offspring, while more than 50% of individuals in the control patches successfully raised offspring. Focal birds in the paired patches exhibited significantly different breeding dispersal behavior. Even though they experienced a reproductive failure, birds in the control patches exhibited a high degree of site fidelity, with over 70% returning to breed in the same patch the next year (Figure 10.7). In contrast, fewer than 50% of the focal birds in the treatment patches returned to breed in the same patch, meaning that more than half exhibited breeding dispersal. Because all focal birds experienced a breeding failure, the research team concluded that birds in the control patches, where patch-wide reproductive success was high, used public information from the reproductive success of others to estimate patch quality and to decide to remain in the same patch the next year. This study provided some of the first experimental evidence that information from conspecifics can affect breeding dispersal decisions.



**FIGURE 10.7. Kittiwake return rates.** Mean (+ SE) return rate of unsuccessful individuals was higher for treatment plots with reproductive success of other birds compared to plots with reproductive failure of other birds. (Source: Boulinier et al. 2008)

So far, we have examined dispersal behavior in light of the benefits and costs of relatively short-distance movements. Next, we use the same approach to understand the evolution of longer, round-trip annual movements, which are seen in many species.

### Video: Black-legged kittiwakes nest

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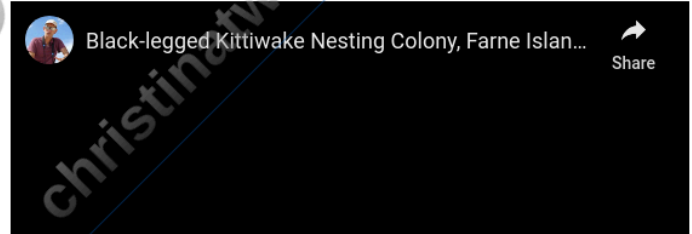
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## 10.3 Individuals migrate in response to changes in the environment

### Learning Objectives

After reading this section, you should be able to

- distinguish migration from dispersal behavior,
- describe how proximate and ultimate factors are involved in migration,
- explain how migration behavior can evolve using a model,
- predict how resource variation should affect migration in species; and
- describe how to examine the heritability of migratory behavior.

Many animals undergo longer, two-way movements known as **migration**. Species in a variety of taxa migrate, including marine invertebrates, insects, amphibians, reptiles, fish, birds, and mammals (Table 10.1). One well-known example is the annual East African migration of more than one million wildebeest (*Connochaetes taurinus*), along with thousands of zebras (*Equus burchelli*) and Thomson's gazelles (*Eudorcas thomsonii*) (Figure 10.8). These animals travel from the southern to northern Serengeti in the spring and return to the southern Serengeti each fall. Over the course of this migration, individuals travel over 400 km (roughly 250 mi), moving from the short-grass plains in the south to savannah habitats in the north and back again.



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**FIGURE 10.8. Wildebeest migration.** Twice each year, wildebeest migrate hundreds of kilometers to more favorable feeding grounds in the Serengeti.

**TABLE 10.1 Examples of migration in different taxa.**

Taxon	Common Name	Species	Route	Distance (KM)
Insect	Dragonfly	<i>Anax junius</i>	New England to Central America	2,800
Crustacean	Blue crab	<i>Callinectes sapidus</i>	Chesapeake Bay	240
Fish	Bluefin tuna	<i>Thunnus thynnus</i>	Atlantic	12,000
Amphibian	Common toad	<i>Bufo bufo</i>	Hibernation site to breeding site	2–3
Reptile	Loggerhead sea turtle	<i>Caretta caretta</i>	California to Japan	11,500
Bird	Arctic tern	<i>Sterna paradisaea</i>	Greenland to Antarctica	19,000
Bird	Blackpoll warbler	<i>Dendroica striata</i>	Alaska to Bolivia	12,000
Mammal	Gray whale	<i>Eschrichtius robustus</i>	Baja, California, to Chukchi Sea	6,000
Mammal	Elephant seal	<i>Mirounga leonina</i>	Sandwich Islands to Antarctica	3,000

(Source: Alerstram, Hedenström, & Åkesson 2003).

The proximate mechanisms involved with the timing of migration vary across taxa and are often related to a combination of internal factors, such as annual rhythms and associated physiological changes, as well as external factors, including changes in photoperiod and local environmental conditions. For example, in the Serengeti, mammals appear to track both the available biomass of grass and its quality. When grass growth slows and grasses dry out during the onset of drought conditions, grass nutritional value drops, and this change may serve as a cue for the onset of migration (Boone, Thirgood, & Hopcraft 2006; Holdo, Hart, & Fryxell 2009; Hopcraft et al. 2014). For birds, the onset of migration is typically triggered by internal physiological changes, whereas the timing and rate of migration are often affected by changes in day length, temperature, and food availability (e.g., Berthold 1993; Marra et al. 2005).

Large-scale movements, however, come at a cost, as the jaeger at the beginning of this chapter illustrates. Not only do long journeys take a physiological toll as a result of the exertion they require, but migrating animals also often suffer risks such as increased predation. Given the costs, what fitness benefits are obtained?

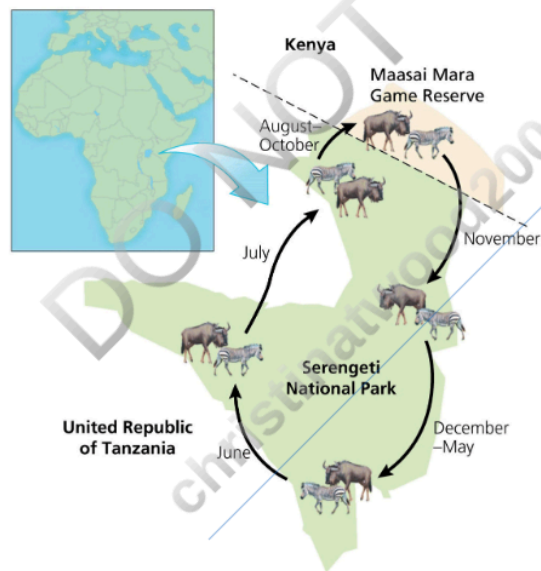
### Migration and changing resources

The benefits of migration include the possibility of moving to an area with more favorable conditions (e.g., more food or water, less extreme temperatures). The decision to stay in one location and forego migration comes with its

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food or water, less extreme temperatures). The decision to stay in one location and forgo migration comes with its own benefits and costs: permanent residents do not pay the costs of long-distance movement but must endure harsher conditions. For migration behavior to evolve in a population, the net benefit of migration must exceed the net benefit of being a permanent resident, and so examining variation in these costs and benefits can help us understand variation in the migratory behavior we see today (Pulido 2007).

Let's go back to the example of wildebeest, zebras, and Thomson's gazelles. These large-bodied herbivores require substantial quantities of grass each day, and grass is dependent on rainfall, which is highly seasonal in the Serengeti. These animals begin the year in the south, feeding on abundant grasses that grow vigorously after the short autumn rainy season. By spring, these grasses are depleted, and the migration begins. The herds move north and west to arrive in the northern Serengeti by July, after the onset of summer rains in this region, and stay until October, when the food supply in the north becomes scarce. At that time, herds begin to move south, back to the southern Serengeti, and arrive in December as the grasses there begin to grow rapidly again (Figure 10.9) (Holdo, Hart, & Fryxell 2009). A similar pattern is seen in many insectivorous birds that breed in temperate regions in summer, when insects are plentiful. These birds migrate south in the autumn as insect availability declines, to overwinter in warmer subtropical regions with higher food abundance, and then return north the following spring to breed. Recent changes in global climate are impacting many migratory species (Applying the Concepts 10.1).



**FIGURE 10.9. Wildebeest migration map.** This map shows the circular migration route of wildebeest over the course of the year.

### APPLYING THE CONCEPTS 10.1

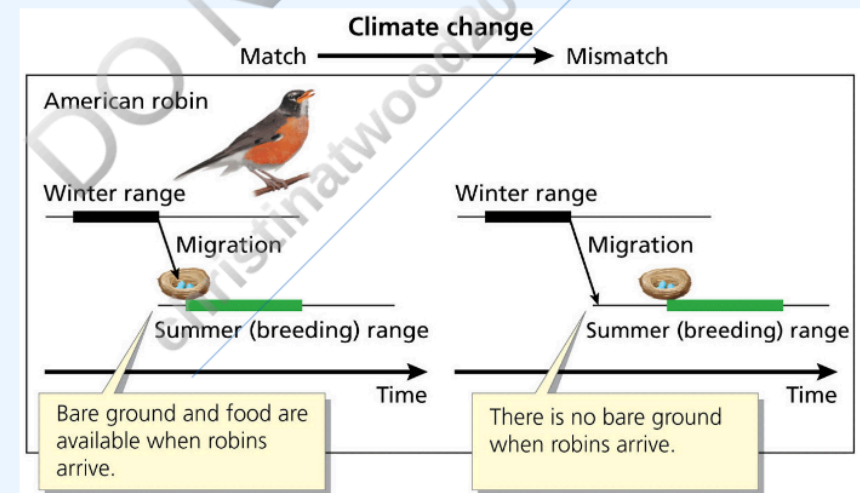
#### Bird migration and global climate change

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*Climate change* is a phrase heard often in the news. The term *climate* refers to statistical averages of temperature, humidity, wind, and rainfall that are based on data collected over decades, whereas *weather* refers to these same parameters from day to day. From 1850 to 1950, the global average temperature fluctuated but exhibited no discernible trend. However, since 1950, the global average temperature has increased dramatically, demonstrating global climate change. Climate change can lead to mismatches between animals and their habitats, and it can have severe consequences for species.

Over the last 50 years, as a warmer climate has developed, particularly in the Northern Hemisphere, spring conditions have been occurring earlier than in the past (Stenseth & Mysterud 2002). For organisms that migrate to follow resources, this shift may result in a mismatch between the migration date and the availability of those resources.

David Inouye and colleagues examined the spring migration return of American robins (*Turdus migratorius*) back to high-altitude sites in the Colorado Rocky Mountains (Inouye et al. 2000). Over the past few decades, spring temperatures have increased, but the average date of snowmelt has not changed (perhaps because of increased snowfall). The research team examined the arrival dates of robins from 1974 to 1999 and the first date of bare ground. They found that robins arrived back from their winter range 14 days earlier over the time period studied. However, snowmelt is now rarely complete when they arrive, and bare ground typically does not appear until 18 days later (Figure 1). This is a problem, because robins need bare ground to search for buried insects. Mismatches resulting from differential responses to climate change can have negative fitness consequences for robins in the Rocky Mountains.



**FIGURE 1. Bird migration and global climate change.** When there is a match between the climate and migration times, robins arrive to find bare ground (green) at their summer breeding range (left). When there is a mismatch as a result of climate change (warmer temperatures), robins arrive earlier but must face snow and no bare ground for 18 days (right). (Source: Stenseth & Mysterud 2002)

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### Video: Robin behavior and natural history

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It's not just robins that are being affected by global climate change. Stephen Mayor and his colleagues have examined changes in the timing of arrival of 48 migratory bird species at their breeding grounds and vegetation green-up in these locations when plants leaf-out ([Mayor et al. 2017](#)). The team used 12 years of satellite data to characterize green-up dates in 200 km × 200 km grids throughout North America and data on arrival days within these grids each year. They estimated bird arrival dates from a large citizen-science observation database. Both green-up

dates on the breeding grounds and arrival dates changed significantly for most of the species, typically advancing by 0.5 to 0.9 days per year over the 12-year period. More importantly, for several species, green-up dates advanced more rapidly than arrival dates, suggesting that migrants were arriving later than peak insect abundance. Such mismatches in cyclical events, driven by differential responses to climate change in plants and birds, may reduce offspring survival and population abundance in these species. ■

### Video: Climate change and bird migration

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## FEATURED RESEARCH Resource variation and migration in neotropical birds

We can hypothesize that migration has evolved in many animal species as an important strategy that allows individuals to (1) take advantage of spatial variation in conditions and (2) avoid seasonal resource depression at different locations. To evaluate this hypothesis, we can test the following prediction: species exposed to a high degree of fluctuation in environmental conditions and resources can benefit by migrating when conditions and resources decline. In contrast, species that live in more stable resource environments have less to gain by migrating and so should be sedentary ([Levey & Stiles 1992](#)).

W. Alice Boyle and Courtney Conway tested this hypothesis using neotropical birds in the clade Tyranni ([Boyle & Conway 2007](#)). This group includes over 300 species of

and colleagues suggest that the migratory behavior of dippers is condition dependent: individuals in the best condition (perhaps dominants) do not migrate and experience high fitness. The researchers did observe four birds that changed their migratory behavior over the course of the study, indicating that migratory behavior is flexible. The results of this study indeed suggest that less competitive individuals are “making the best of a bad job.” These individuals cannot compete with residents for the limited high-quality breeding territories, but they can reproduce—albeit at lower levels than residents—by migrating to higher elevations to breed.

Dippers and many other animals tend to move in a particular direction during migration. For instance, birds in North America tend to migrate south in autumn and north in spring. How do they determine and maintain their direction? We answer that question next.

## 10.4 Environmental cues and compass systems are used for orientation when migrating

### Learning Objectives

After reading this section, you should be able to

- differentiate between orientation and navigation,
- explain the sun and geomagnetic compass, and
- design a test to examine the use of each compass.

Animals that migrate long distances face two issues: (1) **orientation**, or maintaining the proper direction of travel; and (2) **navigation**, or determining how to reach a particular destination. In the 1950s, Gustav Kramer suggested that birds migrate long distances by use of a “compass and map” system ([Kramer 1952](#)). He meant that birds can orient in the proper direction and find particular locations using mental maps, much as people use physical maps ([Schmidt-Koenig 1979](#)). In the decades since, research has indicated that many animals, not just birds, use a variety of compass systems to orient to a particular direction, and some appear to also possess a mental map that is used to find particular locations. In this section, we examine orientation. In the last section of the chapter, we turn our attention to navigation and mental maps.

### Compass systems

A variety of environmental cues can provide directional information for orientation. One type of cue used by a variety of migratory animals, including insects, fish, amphibians, birds, and mammals, is a physical landmark, such as a coastline, island, river system, or distant mountain (e.g., [Collett & Graham 2004](#)). It has long been known that some marine mammals and shorebirds migrate along continental coastlines. For instance, gray whales (*Eschrichtius robustus*) in the eastern North Pacific migrate up to 20,000 km from their summer feeding grounds in the Chukchi Sea off the coast of Alaska to their calving grounds off the coast of Baja, California ([Figure 10.16](#)).

in the Chukchi Sea off the coast of Alaska to their calving grounds off the coast of Baja, California (Figure 10.16).

During migrations north and south, whales generally remain close to the coastline, particularly when mothers are traveling north with their calves (Poole 1984).



**FIGURE 10.16. Whale migration.** (a) Gray whale. (b) Whales use the coastline for orientation during their migration. Blue indicates southbound migration, and orange indicates northbound migration.

Many migratory animals orient using systems such as a **sun compass**—the use of the location of the sun in the sky (Wehner 1998; Åkesson & Hedenström 2007). Each day, the sun rises in the east and sets in the west, so its position in the sky relative to the time of day provides accurate directional information. Experiments reveal that invertebrates, fish, amphibians, reptiles, birds, and mammals use a solar compass (Wehner 1998; Åkesson & Hedenström 2007). Even on cloudy days, many of these animals can use the pattern of polarized skylight to determine the position of the sun, although the mechanisms of this process are not fully understood (Wehner 2001).

Nocturnal animals or those that move at night can use a **star compass**, because the constellations rotate around the celestial pole (Figure 10.17). A series of experiments by Steve Emlen demonstrated that hand-reared birds can learn to orient based on the rotation of stars in the night sky (Emlen 1967a; Emlen 1967b) (Toolbox 10.1). Subsequent work has revealed that many other taxa, including invertebrates, fish, amphibians, reptiles, and mammals, also use a star compass for orientation.



**FIGURE 10.17. Star compass.** Time-lapse photography shows how the stars appear to rotate around Polaris in the northern sky in the Northern Hemisphere. Each streak is a star.

#### TOOLBOX 10.1 Emlen funnels

Early observations about bird migration indicated that caged birds increased their activity levels each spring and fall, a behavior known as migratory restlessness, or *Zugunruhe*. Stephen Emlen studied this behavior in a series of classic experiments using indigo buntings (*Passerina cyanea*). Indigo buntings are beautiful blue birds that breed each spring in the eastern United States and then migrate to spend the winter in southern Mexico, Central America, and the Bahamas. Interestingly, these birds are normally diurnal, except during the migration season, when they become highly active in the evening and throughout the night. These observations suggested that perhaps these birds were using celestial cues such as stars to orient.

Emlen designed a simple yet elegant apparatus to take advantage of the buntings' migratory restlessness behavior (Emlen & Emlen 1966) (Figure 1). An Emlen funnel consists of a small funnel with a wire mesh top that allows a bird to see out. The bottom has an inkpad that transfers ink to a bird's feet. The sides of the funnel are lined with paper. A bird's movements in hopping forward as it exhibits migratory restlessness are recorded by the ink tracks left by its feet on the paper.

#### Video: Orientation cage experiment with sharp-tailed sandpiper

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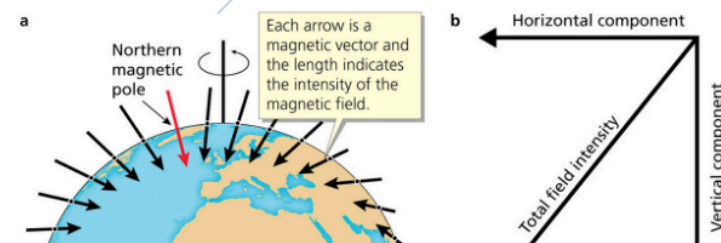
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**FIGURE 1.** Emlen funnel. Side view of an Emlen funnel, showing an Indigo bunting (*Passerina cyanea*) standing on an inkpad. Its footprints are then recorded on the paper sides. (Source: [Emlen & Emlen 1966](#))

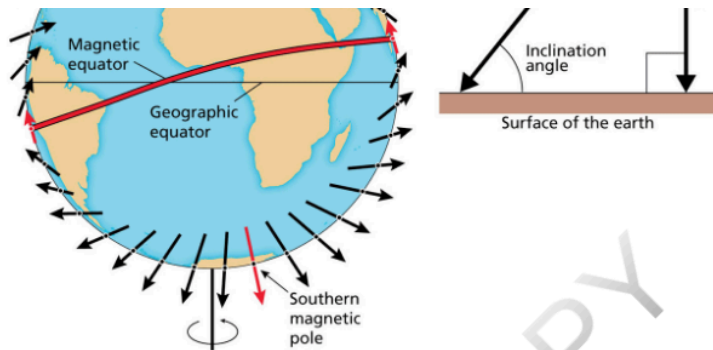
Emlen conducted experiments in a planetarium, where he could manipulate the night sky to examine how it affected the birds' orientation and movements ([Emlen 1967a](#); [Emlen 1967b](#)). Stars can provide directional information in the Northern Hemisphere, because all stars rotate around the celestial pole. In a series of experiments, he placed birds in Emlen funnels and manipulated the location of stars and their rotation. He convincingly showed that indigo buntings use celestial cues for orientation. In particular, he determined that maturing birds learn to identify the direction around which all stars rotate and use this fixed location as an indicator of north. In the Northern Hemisphere, the celestial pole is centered on the North Star, Polaris. Emlen demonstrated that he could train young birds to use a different star (Betelgeuse, in the constellation Orion) as an incorrect indicator of north after he allowed birds to view all stars in the planetarium rotating around it ([Emlen 1970](#)). More recent research indicates that indigo buntings may also use the earth's magnetic field to orient in the proper direction during migration ([Sandberg et al. 2000](#)).

The earth's magnetic field provides another source of directional information for animals ([Figure 10.18](#)). These fields flow from the south magnetic pole to the north magnetic pole. Animals can therefore use a **geomagnetic compass**, or the ability to orient using the earth's magnetic field. Recall from [Chapter 5](#) that the magnetic field provides directional information in three ways. First, it flows in one direction—from south to north. Second, the angle of inclination with respect to the horizontal varies with latitude. Third, the intensity of the field tends to be strongest at the poles and weakest at the magnetic equator. Use of a geomagnetic compass has been documented in dozens of species in many taxa, including snails, crustaceans, insects, fish, amphibians, reptiles, birds, and mammals ([Wiltchko & Wiltchko 2005](#)).



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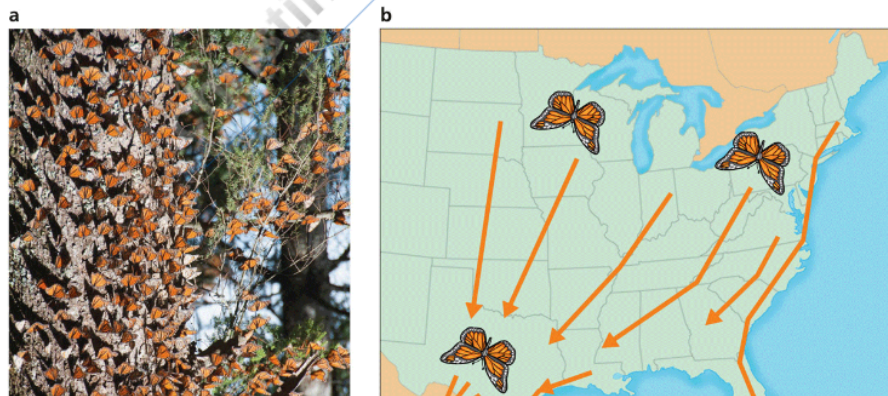


**FIGURE 10.18. Magnetic field of the earth.** (a) The magnetic vectors around the earth. Arrows indicate the local vector and angle of inclination; their length indicates the intensity (strength) of the field. (b) The total field intensity is composed of a horizontal component and a vertical component. (Source: [Willischko & Willischko 2005](#)) (Source: [Lohmann, Putnam, & Lohmann 2008](#))

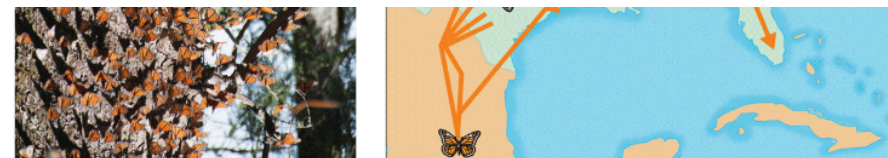
Next, we examine two examples illustrating how researchers study the use of compass systems for migratory orientation.

## FEATURED RESEARCH Antennae and the sun compass system in monarchs

One intensely studied animal that uses the sun compass in its annual migration is the monarch butterfly. Monarch butterflies (*Danaus plexippus*) in central and eastern North America migrate to a few mountaintop sites in central Mexico, where millions of individuals gather in massive clusters to spend the winter ([Davis & Rendón-Salinas 2010](#)). Depending on the starting location, this journey can take several weeks and cover over 1,000 km ([Figure 10.19](#)).



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**FIGURE 10.19. Monarch migration.** (a) Monarch cluster. (b) Autumn migration routes of eastern monarch butterflies to wintering grounds in Mexico.

The monarch generation that migrates to Mexico in the fall will not return to its natal area in the spring. Instead, many generations are produced during the spring migration—a cycle known as **intergenerational migration**. The first generation stops in northern Mexico and the southern United States, where the butterflies mate, lay eggs, and die. The emerging generation heads farther north and again mates, lays eggs, and dies. This pattern is repeated several times as each generation moves farther north ([Reppert & Roode 2018](#)). This raises a critical question: How do butterflies that have never been to their wintering site get there?

### Video: Monarch butterfly migration

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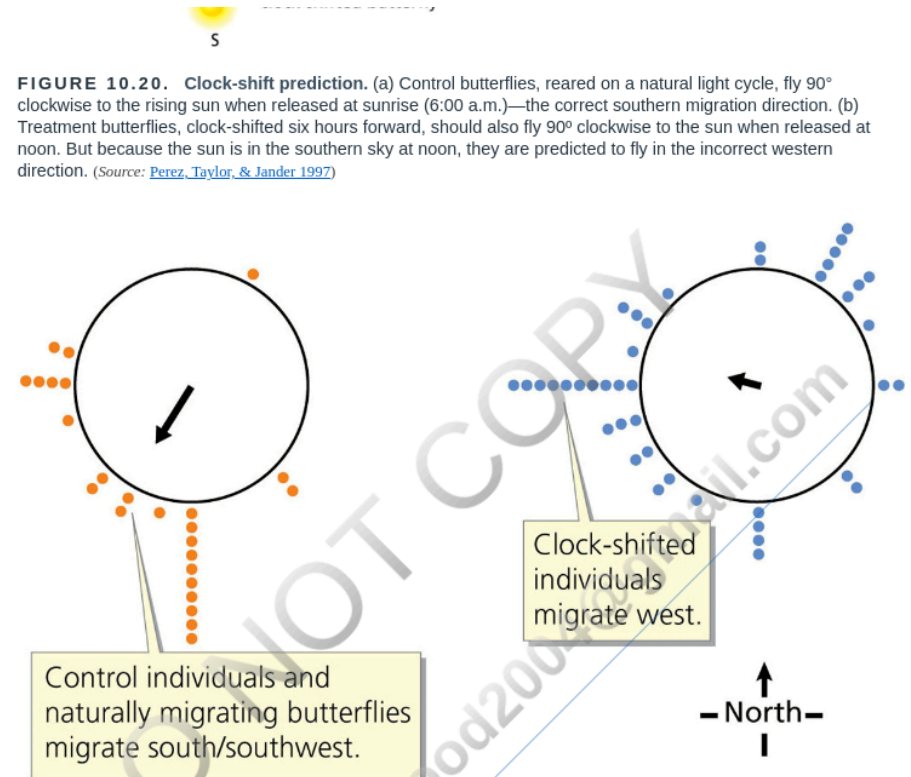
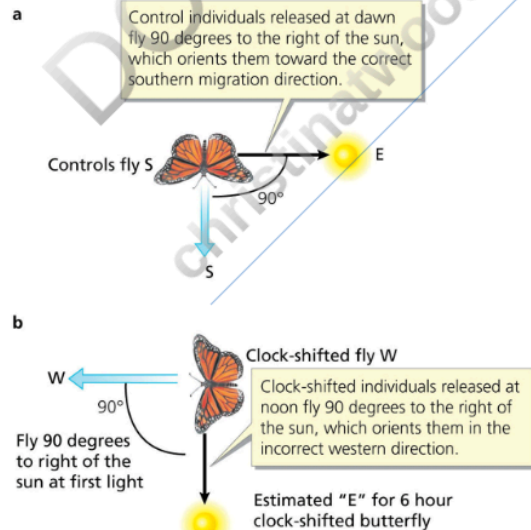
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Animals, including monarchs, have internal timekeeping mechanisms that regulate such daily activities as their active and resting cycles. The internal clock is itself regulated by daily light and dark cycles. After a 12-hour dark cycle (and at the beginning of a light cycle), the position of the sun provides directional information, because the sun rises in the eastern sky. In the autumn, after six hours of daylight, the sun has moved to the southern sky (in the Northern Hemisphere), and at the end of a 12-hour light cycle, the position of the sun provides information about the direction west.

A simple “clock-shift” experiment demonstrated that monarchs use a sun compass by bringing two groups of these butterflies into the laboratory (Perez, Taylor, & Jander 1997). One group was “clock-shifted” six hours over the course of several weeks (Figure 10.20). That is, these individuals still experienced a light/dark cycle of 12 hours each, but their lights were turned on at a later time each day until eventually the lights came on at noon, when the sun outside was in the southern sky in the autumn. The control group was kept on the naturally occurring light/dark cycle, so their lights were turned on at 6:00 a.m. Both groups were then released outside (just after their lights turned on) in September and were followed. The control group migrated south/southwest, as is typical in Kansas, where the work was conducted. In contrast, the clock-shifted animals moved in a westward direction. Why? Their internal clock had been reset so that their “daybreak” occurred at noon. At noon, the sun was in the southern sky, but they interpreted this position as east—the normal direction of the sun at daybreak—and so migrated in the wrong direction (Figure 10.21).



**FIGURE 10.20. Clock-shift prediction.** (a) Control butterflies, reared on a natural light cycle, fly 90° clockwise to the rising sun when released at sunrise (6:00 a.m.)—the correct southern migration direction. (b) Treatment butterflies, clock-shifted six hours forward, should also fly 90° clockwise to the sun when released at noon. But because the sun is in the southern sky at noon, they are predicted to fly in the incorrect western direction. (Source: Perez, Taylor, & Jander 1997)

Christine Merlin, Robert Gegear, and Steven Reppert investigated whether antennae play a role in the monarch’s sun compass (Merlin, Gegear, & Reppert 2009) (Scientific Process 10.2). They examined migratory orientation by tethering individuals in an outdoor flight simulator during fall migration. They first compared the flight direction movement behavior of controls, whose antennae were intact, and that of individuals that had had their antennae removed. Individuals without antennae could fly, but they failed to orient to any particular direction—just as many tried to move north as tried to move south. In contrast, the flight direction of control butterflies was to the south/southwest, the proper direction for migration in early October.

#### Video: Tethered monarch butterfly in flight simulator

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Video: Tethered monarch butterfly in flight simulator

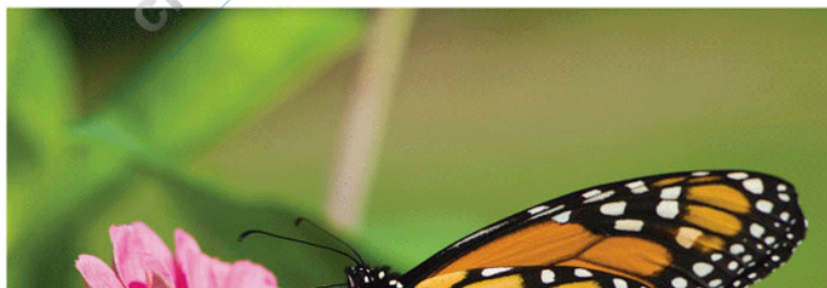
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## SCIENTIFIC PROCESS 10.2

### The role of the antennae in the monarch butterfly sun compass



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Research Question: *How do monarch butterflies use a sun compass?*

### Hypothesis (1):

The sun compass is associated with the antennae.

### Prediction (1):

Individuals without antennae will not be able to orient properly.

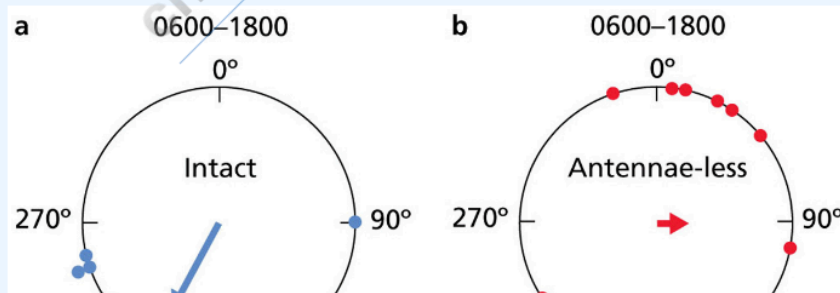
### Methods (1):

The researchers:

- Removed antennae from ten butterflies (antennae-less treatment) and left the antennae of ten control butterflies intact
- Tethered individuals and recorded flight behavior direction

### Results (1):

Control butterflies oriented south/southwest, while antennae-less butterflies did not orient in any particular direction.



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**FIGURE 1. Antennae results.** Flight orientation of (a) intact and (b) antennae-less butterflies between 0600 (6:00 am) and 1800 (6:00 pm). (Source: [Merlin, Gegear, & Reppert 2009](#))

### Hypothesis (2):

Antennae contain photoreceptors needed for proper orientation.

### Prediction (2):

Butterflies with clear paint or no paint on their antennae will be able to orient properly, whereas butterflies with black paint on their antennae will not be able to orient properly.

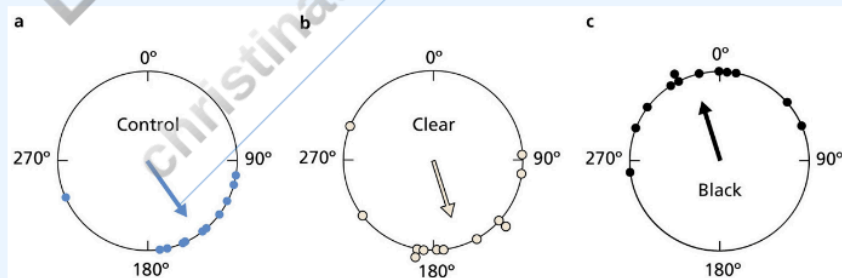
### Methods (2):

The researchers:

- Painted butterflies' antennae with opaque black paint, clear paint (Control 1), or no paint (Control 2)
- Tethered individuals and recorded flight behavior direction

### Results (2):

Butterflies with no paint or clear paint on their antennae oriented south/southeast. Butterflies with black-painted antennae oriented north.



**FIGURE 2. Paint results.** Flight orientation of (a) controls, (b) individuals with clear-painted antennae, and (c) individuals with black-painted antennae. (Source: [Merlin, Gegear, & Reppert 2009](#))

### Conclusions:

Antennae and functioning photoreceptors are required for sun compass orientation in monarch butterflies.

### Evaluate

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To determine whether these results were due to differences in light reception in the antennae, the researchers conducted a second set of experiments a few weeks later, from mid-October to mid-November. This time, they painted antennae either an enamel-based black or clear. The black paint blocked perception of light, while the clear paint allowed light to pass through to the antennae. They again examined the flight direction of tethered individuals in the outdoor flight simulator. The movement behavior of individuals whose antennae were painted with clear paint was to the south/southeast (the proper direction at that time of the year), whereas individuals whose antennae were painted black attempted to move to the north/northwest. The lack of proper movement is

whose antennae were painted black attempted to move to the north/northwest. The lack of proper movement in individuals with either no antennae or black-painted antennae that blocked light indicates that antennae photoreceptors are crucial to this species' sun compass.

Studies such as this demonstrate how migrating butterflies orient in the proper direction to reach their wintering grounds in Mexico. However, much work still needs to be done to understand how these individuals reach their specific destination. Part of this effort involves the use of citizen scientists all over North America, who collect data each year on migrating butterflies ([Applying the Concepts 10.2](#)).

## APPLYING THE CONCEPTS 10.2

### Citizen scientists track fall migration flyways of monarch butterflies

Monarch butterflies are of concern to conservation biologists because of the loss of their required habitat in Mexico, the United States, and Canada. To better monitor monarch butterfly populations, researchers engage citizen scientists to help collect data on the butterflies' life stages. Citizen scientists are individuals, such as yourself, who are trained by biologists to participate in field projects across the country. The monarch butterfly project includes the [Monarch Larva Monitoring Project](#), in which individuals at nature centers throughout the United States learn to conduct weekly surveys of monarch eggs and larvae on plants. [Monarch Watch](#), based at the Kansas Biological Survey at the University of Kansas, oversees numerous citizen scientist programs that involve tagging individual butterflies and creating monarch waystations.

One monarch watch program, [Journey North](#) collects citizen scientist reports of monarch sightings during the fall migration. Elizabeth Howard and Andrew Davis used three years of these data to examine the migration flyway of monarchs in eastern North America ([Howard & Davis 2009](#)). Their analysis of thousands of sightings indicates that there is one major flyway south through the central portion of the United States ([Figure 1](#)).

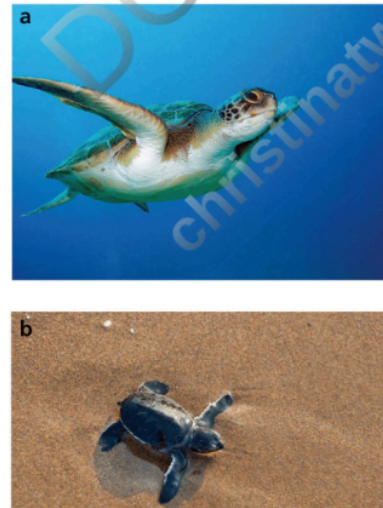


**FIGURE 1. Citizen scientists.** The dots represent roost sightings of monarchs reported by citizen scientists from 2005 to 2007. The star represents the location of the overwinter site in Mexico. The central flyway is to the left of the green line. (Source: [Howard & Davis 2009](#))

This is important information, because it allows scientists to know where to concentrate habitat conservation efforts. Such information is the direct result of data collection by citizen scientists. If you want to become a citizen scientist, visit the website of the [USDA Forest Service](#) for more information. ■

## FEATURED RESEARCH The magnetic compass in sea turtles

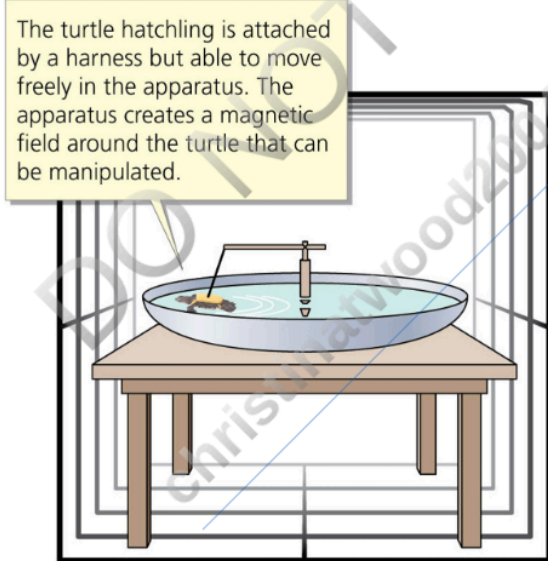
Many species migrate between breeding and feeding sites that may be thousands of kilometers apart. Loggerhead sea turtles (*Caretta caretta*) ([Figure 10.22](#)) lay eggs in underground nests on sandy beaches. Turtle hatchlings from southern Florida emerge and, after traveling to the water, must orient toward their feeding grounds in a large, circular system of ocean currents called the North Atlantic gyre. For loggerhead sea turtle hatchlings, this journey takes several days. Once at the feeding grounds, individuals may spend several years in the ocean, until sexual maturity, when they migrate back to their natal beaches for nesting ([Lohmann, Putnam, & Lohmann 2008](#)).





**FIGURE 10.22. Loggerhead sea turtle.** (a) An adult turtle migrating in the ocean. (b) A hatchling.

Kenneth and Catherine Lohmann and colleagues have studied sea turtles for over 20 years (e.g., [Lohmann et al. 2001](#)). In an early study, Kenneth Lohmann tested the ability of juvenile loggerhead sea turtles to detect and orient using magnetic fields. He used an apparatus to reverse the polarity of the magnetic field experienced by turtles ([Lohmann 1991](#)). The apparatus consisted of an open chamber with a walking table, encircled by a large coil that could create a strong magnetic field ([Figure 10.23](#)). Individuals were attached to a harness that allowed them to orient and swim in any direction while the apparatus recorded their individual movements and orientation during a trial. One set of turtles was placed in the chamber while the magnetic field was reversed; a control set experienced the normal magnetic field. Turtles in the control treatment oriented and moved to the northeast, the direction of the North Atlantic gyre, and those that experienced a reversed magnetic field oriented and moved in the opposite direction ([Figure 10.24](#)). Thus, both groups oriented and moved toward a magnetic north, demonstrating the use of a geomagnetic compass.



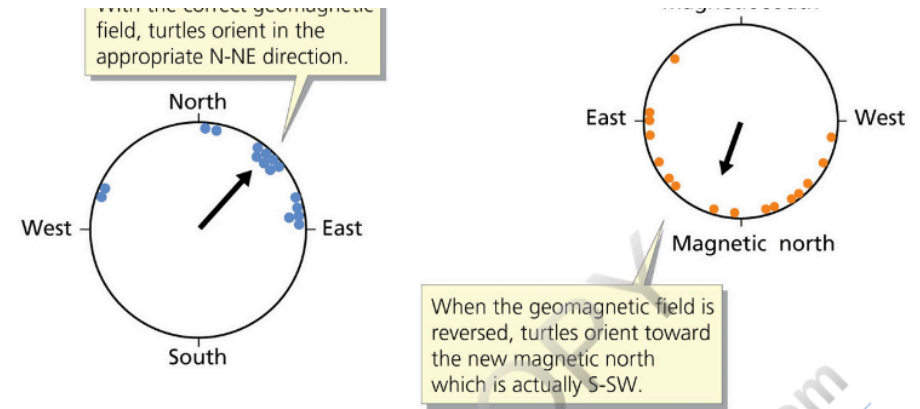
**FIGURE 10.23. Turtle orientation apparatus.** Diagram of the apparatus used to characterize orientation direction of sea turtles. The magnetic field inside the apparatus can be changed. (Source: [Lohmann 1991](#))

#### a Geomagnetic Field

With the correct geomagnetic

#### b Reversed Field

Magnetic south



**FIGURE 10.24. Turtle orientation.** (a) Control turtles attempted to move north/northeast. (b) When the magnetic field was reversed, turtles attempted to move toward the new position of magnetic north. Each dot represents data for one turtle, and the mean direction is indicated by the arrow. (Source: [Lohmann 1991](#))

#### Video: Sea turtle migration research

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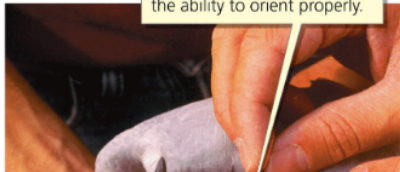
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## Multimodal orientation

The previously described research illustrates how researchers have demonstrated the use of different compass systems. But one particular aspect is important to note: most, if not all, animals use multiple cues to orient ([Mouritsen 2018](#)). For instance, much research has examined the homing behavior of rock doves (*Columba livia*), commonly known as pigeons. Most studies of pigeon homing allow birds to live in a home loft for several weeks. Birds are then displaced to a new location, and the flight direction or the entire flight of released birds is recorded using radio tags or flight recorders. This domesticated species has a remarkable ability to find its way back to a home roost after being displaced up to 1,800 km. How do they do this?

Pigeons that are temporarily blinded can orient properly and return home, so vision is not required to orient properly ([Walcott 2005](#)). However, birds that are clock-shifted six hours fly in the wrong direction—they make a 90° error in their orientation ([Schmidt-Koenig 1990](#)), just as we saw for monarch butterflies. This finding demonstrates that pigeons use a sun compass to orient. However, this error only occurs if birds can see the sun; on overcast days, clock-shifted birds orient in the proper direction ([Keeton 1974](#)), indicating that pigeons use another cue to orient when the sun is hidden behind clouds. To investigate the possibility that pigeons use a magnetic compass, researchers placed magnets on their back ([Figure 10.25](#)) or magnetic coils on their head to alter the magnetic field around each bird. Such birds failed to orient properly, but only when they could not see the sun ([Walcott 1996](#)). Other work has shown that pigeons that are made anosmic (i.e., lack functioning olfaction) fail to orient properly when released at unfamiliar locations, suggesting a role for olfaction in orientation ([Wiltschko & Wiltschko 1989](#); see also, Gagliaro et al. 2013). These studies demonstrate that birds can use multiple cues to orient properly. Such redundancy is likely widespread across taxa because it provides backup mechanisms that help animals to travel in the proper direction ([Endres et al. 2016](#); [Mouritsen 2018](#)).

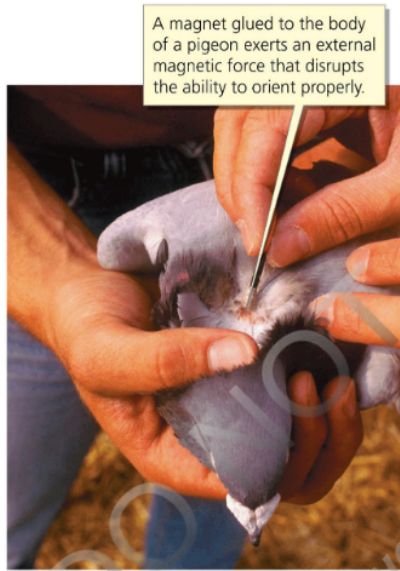
A magnet glued to the body of a pigeon exerts an external magnetic force that disrupts the ability to orient properly.



**FIGURE 10.25. Pigeon magnetoreception.** When small magnets are placed on their body, pigeons have trouble orienting properly.

The ability to orient is just one aspect of migration. Animals also need to be able to move to specific locations, like the sea turtles that need to return to their natal beach to nest. Next, we examine how animals accomplish such navigation.

back (Figure 10.25) or magnetic coils on their head to alter the magnetic field around each bird. Such birds failed to orient properly, but only when they could not see the sun (Walcott 1996). Other work has shown that pigeons that are made anosmic (i.e., lack functioning olfaction) fail to orient properly when released at unfamiliar locations, suggesting a role for olfaction in orientation (Wiltschko & Wiltschko 1989; see also, Gagliaro et al. 2013). These studies demonstrate that birds can use multiple cues to orient properly. Such redundancy is likely widespread across taxa because it provides backup mechanisms that help animals to travel in the proper direction (Endres et al. 2016; Mouritsen 2018).



**FIGURE 10.25. Pigeon magnetoreception.** When small magnets are placed on their body, pigeons have trouble orienting properly.

The ability to orient is just one aspect of migration. Animals also need to be able to move to specific locations, like the sea turtles that need to return to their natal beach to nest. Next, we examine how animals accomplish such navigation.

## 10.5 Bicoordinate navigation allows individuals to identify their location relative to a goal

### Learning Objectives

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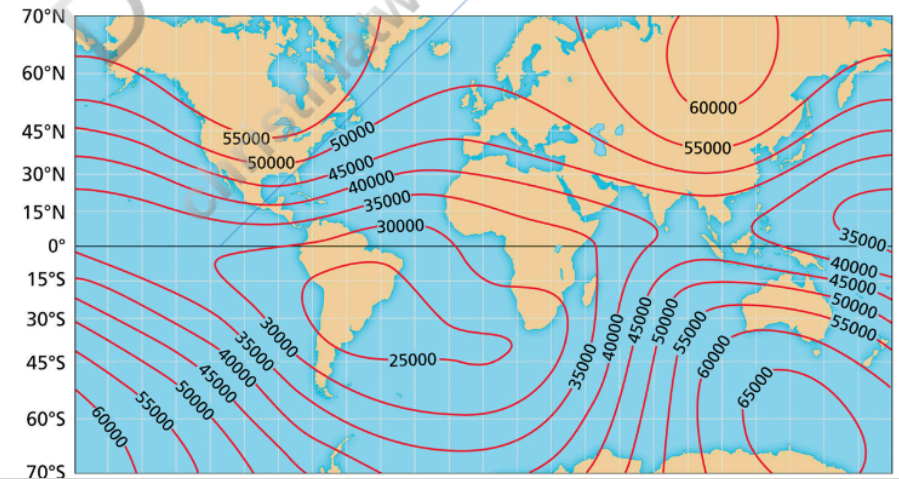
- define bicoordinate navigation and
- summarize the study showing that Eurasian reed warblers are capable of bicoordinate navigation during migration.

Some migrating animals are capable of **bicoordinate navigation**: they can identify their geographic location using two varying environmental gradients, much as humans use latitude and longitude. As an animal migrates, its geographic location changes. As long as it knows its present location relative to a target location or goal, such as its starting point or its final destination, it can adjust its direction to arrive at the destination. An important feature of bicoordinate navigation is that it can be used even when an individual is in an unfamiliar location, as might occur when it is blown off course during migration. Because bicoordinate navigation provides positional information, it is often referred to as a mental map.

Here we briefly examine three examples of bicoordinate navigation. We begin by revisiting the work of the Lohmanns and colleagues to see how they determined that sea turtles use bicoordinate navigation and a mental map.

### FEATURED RESEARCH Bicoordinate navigation in sea turtles

Recall that the angle of inclination of the earth's magnetic field changes with latitude (Figure 10.18). In addition, the intensity of the magnetic field also varies across the globe (Figure 10.26). Because these aspects provide two environmental gradients, they can be used for bicoordinate navigation.



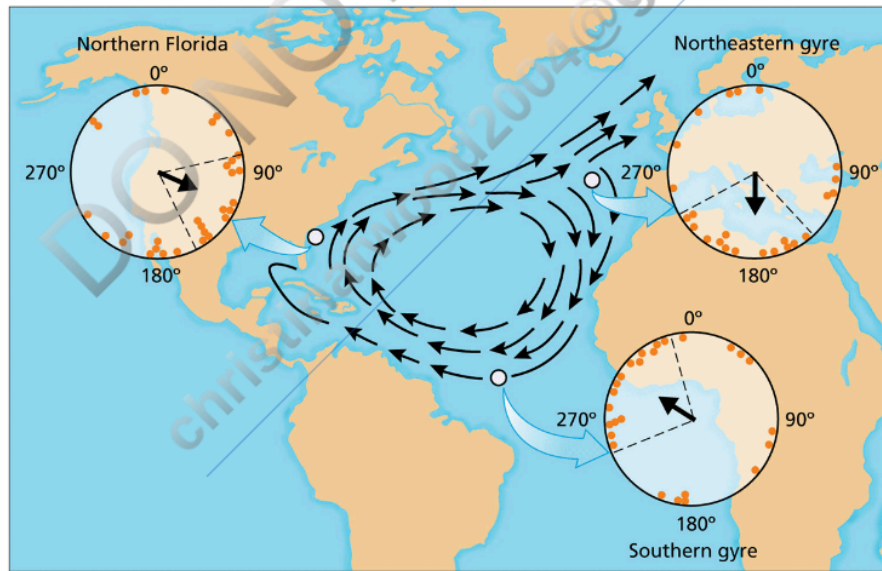
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**FIGURE 10.26. Intensity of the earth's magnetic field.** Lines indicate variation in the intensity of the magnetic field, measured in nanoteslas (nT). Intensity ranges from about 25,000 to 65,000 nT.

To determine whether sea turtles use bicoordinate navigation, the Lohmanns took advantage of an important fact: turtles need to orient themselves in order to remain in the North Atlantic gyre. For example, near Portugal, a northward current springs off the gyre and runs toward the colder northern waters of England. If sea turtles end up in these colder waters, they will die, and so turtles near Portugal need to move south. But turtles in the South Atlantic need to move north to remain in warm water.

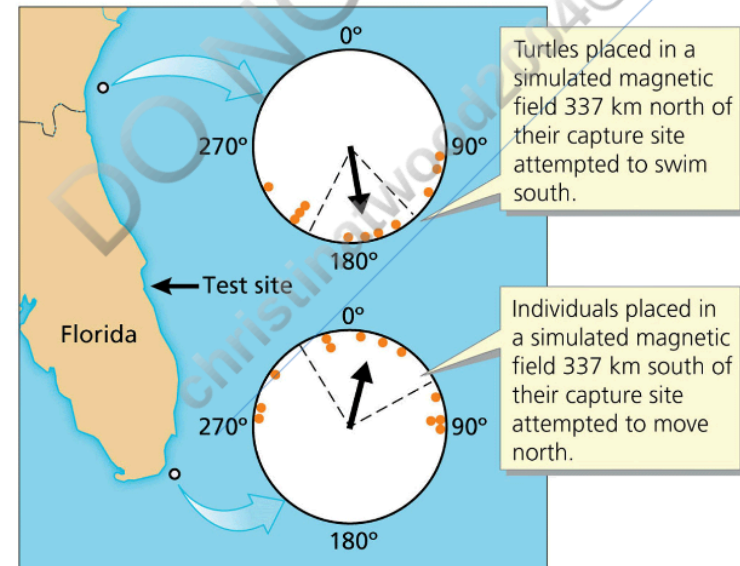
The Lohmanns and colleagues (Lohmann et al. 2001) tested the ability of loggerhead sea turtle hatchlings to orient in the gyre. The experiment, conducted in eastern Florida, again used a computerized coil system to control the magnetic field. Turtles were exposed to one of three different magnetic fields that were characteristic of three different geographic locations in the North Atlantic gyre, thanks to variations in the angle of inclination and field intensity. The hatchlings all oriented to stay within the gyre at each of the perceived locations (Figure 10.27). This finding indicates that migrating sea turtles can use the earth's magnetic field to orient in different (and appropriate) directions. In addition, because hatchlings that had no prior experience could navigate properly, this ability must be inherited and not learned.



**FIGURE 10.27. Sea turtle gyre results.** The North Atlantic gyre is represented by the circular arrows. Each large circle represents orientation data from individual turtles (orange points) at the geomagnetic fields of three geographic locations (small white circles). The means are indicated by the black arrows. (Source: Lohmann et al. 2001)

To further investigate bicoordinate navigation in sea turtles, the Lohmanns and colleagues examined whether green sea turtles (*Chelonia mydas*) use variation in the earth's magnetic field to navigate to specific locations (Lohmann et al. 2004). They captured juveniles near Melbourne, Florida, and transported them to an orientation apparatus at a nearby test site. In this species, juveniles remain in shallow coastal feeding grounds near their natal beach for an extended period. The researchers took advantage of this fact and divided the turtles into two groups. One group was exposed to a magnetic field that simulated the magnetic conditions 337 km north of the capture location. The other group of turtles was exposed to a magnetic field that simulated the magnetic conditions 337 km south of the capture location. Such "displaced" turtles would be expected to try to swim back to their feeding ground. Turtles were allowed to orient and move freely within the apparatus, and the directions in which they swam were recorded.

The research team found that the turtles in the two test groups behaved in different ways. Those experiencing simulated conditions of an area 337 km north of the capture site oriented and tried to move south, while those experiencing simulated conditions of an area 337 km south of the capture site oriented and tried to move north (Figure 10.28). These results show that sea turtles can use variation in the earth's magnetic field as a map to guide navigation north and south to a specific location—in this case, back toward their capture site. But how do individuals return to a specific location? Recent work has indicated that individuals appear to learn the magnetic field signature of their natal home area, a form of geomagnetic imprinting. Because the Earth's magnetic field varies predictably across the globe, individuals can then rely on their magnetic navigation ability to return home to breed (Brothers & Lohmann 2018; Lohmann & Lohmann 2019).



**FIGURE 10.28. Orientation of displaced turtles.** Turtles placed in magnetic fields that simulated magnetic conditions north or south of the capture site attempted to return to their site of capture. The mean orientation is indicated by each arrow. (Source: Lohmann et al. 2004)



Turtles are not the only animals capable of bicoordinate navigation, as we see next.

## FEATURED RESEARCH Bicoordinate navigation in birds

Many birds migrate thousands of kilometers and use a geomagnetic compass, a sun compass, or a star compass (for a review, see [Wiltschko & Wiltschko 2009](#)). But do birds display bicoordinate navigation? To answer this question, Nikita Chernetsov, Dmitry Kishkinev, and Henrik Mouritsen examined migration movements in Eurasian reed warblers (*Acrocephalus scirpaceus*), which spend the winter in sub-Saharan Africa and then migrate to Eurasia to breed.

Chernetsov and colleagues conducted an experiment during the warblers' spring migration ([Chernetsov, Kishkinev, & Mouritsen 2008](#)). Over a period of three years, they captured individuals near Rybachy, Russia. Half were flown 1,000 km east to Zvenigorod, while the other half were kept in Rybachy ([Figure 10.29](#)). The birds were placed in small Emlen funnels, an apparatus developed by Stephen Emlen to study use of the star compass in birds ([Toolbox 10.1](#)). The test birds had a clear view of the sky and so could use a variety of compass cues ([Figure 10.30](#)).

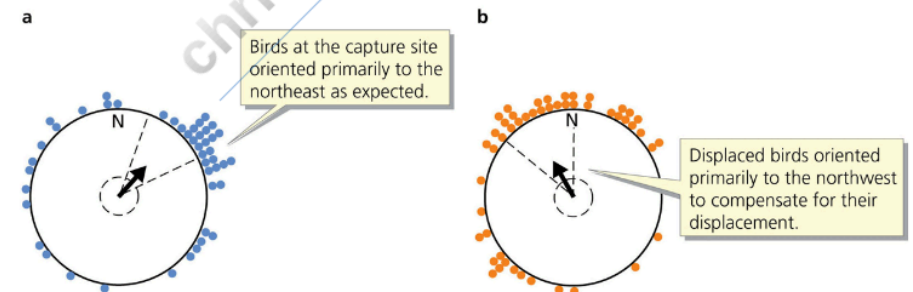


**FIGURE 10.29. Displacement predictions.** Birds migrating northeast (to the destination indicated by the red star) were displaced 1,000 km east from Rybachy to Zvenigorod. They could travel in one of three directions (dashed lines): (1) west, (2) northeast, or (3) northwest. (Source: [Chernetsov, Kishkinev, & Mouritsen 2008](#))



**FIGURE 10.30. Reed warbler migration.** (a) The Emlen funnels used by Chernetsov and colleagues to study migratory movement in the field. (b) Eurasian reed warbler.

The Eurasian reed warblers tested at the capture site oriented northeast, the direction of their destination. The birds displaced 1,000 km east from Rybachy to Zvenigorod could exhibit one of three behaviors: (1) they might orient due west, trying to return to the capture site, as we saw in green sea turtles; (2) they might orient northeast, the direction they were originally heading; or (3) they might orient northwest, trying to navigate to their final destination. The research team found that displaced birds oriented to the northwest and so were orienting in a new direction to compensate for being displaced, suggesting that they, too, have the capacity for bicoordinate navigation ([Figure 10.31](#)). These results suggest that Eurasian reed warblers are able to determine their geographic position and adjust their migration route after being displaced, much as we use maps to find our way home after getting lost—although it is still unclear how they do this. Obviously, this ability can be of adaptive significance if birds are blown off course or need to modify their migratory route.



**FIGURE 10.31. Orientation results.** (a) Orientation of birds at the capture site, predominantly to the northeast.

**FIGURE 10.31. Orientation results.** (a) Orientation of birds at the capture site, predominately to the northeast. (b) Orientation of birds at the displacement site, predominately to the northwest. Arrows indicate mean direction of orientation in each case. (Source: [Chernetsov, Kishkinev, & Mouritsen 2008](#))

One final set of well-known migrants includes salmon and their relatives. We end by examining how these fish accomplish their navigational feats.

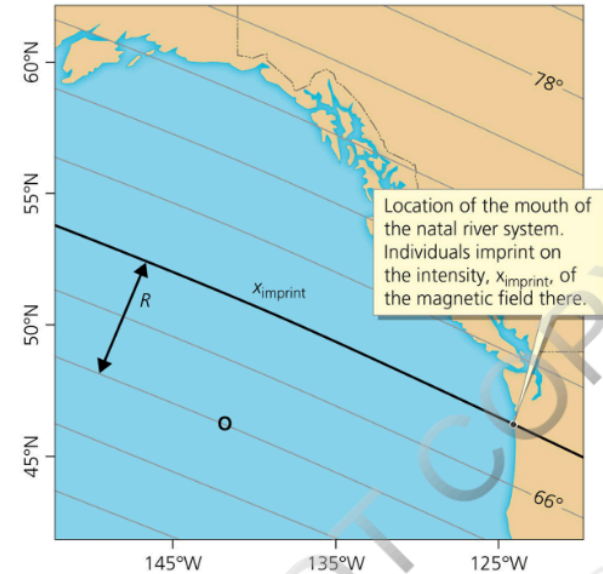
## FEATURED RESEARCH Homing migration in salmon

Salmonids (salmon, char, and trout) are well known for their ability to return to their natal stream to spawn. Many salmon migrate downstream to the ocean, where they spend up to several years feeding prior to their long journey home to reproduce. This journey can be up to thousands of kilometers long and can occur more than ten years after leaving the natal stream. How is this feat accomplished?

Two mechanisms are thought to be used in this migration: olfaction and geomagnetic reception. Both rely on imprinting, which is thought to occur when salmon undergo a physiological change that allows them to adapt to both freshwater and saltwater—a process known as smoltification. Smoltification is associated with increases in several hormones, including thyroxine, which is thought to be associated with olfactory imprinting of the natal stream ([Dittman & Quinn 1996](#)). In essence, fish are thought to learn the odor and the magnetic properties of their natal stream in order to return to it ([Lohmann & Lohmann 2019](#)).

The olfaction imprinting hypothesis was first proposed by Arthur Haesler and Warren Wisby and assumes that streams possess a characteristic and persistent odor, that fish can detect such odors, and that fish retain a memory of the odor they experience early in life ([Haesler & Wisby 1951](#)). Haesler and Wisby demonstrated the importance of olfaction in a simple experiment in which they captured salmon migrating upstream from two forks of a Y-shaped stream near Seattle ([Wisby & Haesler 1954](#)). Each fish was uniquely tagged to identify the fork in which it was captured. Half the fish had their olfactory pits blocked to impair their olfactory sense, and the other half (controls) were left untreated. All individuals were then released 1.6 km below the fork so that they could resume their migration upstream. Of the fish recaptured, 89% of controls but only 40% of treatment fish were captured in the same branch in which they were originally captured. The researchers concluded that olfactory-impaired fish randomly selected a fork, whereas those with functioning olfaction used that sense to return to their natal stream. What exactly provides the unique odors of natal streams is less clear. Some work points to amino acids ([Yamamoto, Hino, & Ueda 2010](#)), while other work suggests that salmon detect the odor of related, younger fish moving downstream ([Nordeng 1977](#)).

For adult salmon in the open ocean, the first need is to find the mouth of their natal river system. It is difficult to do this using odor alone, and so a second mechanism is needed: this may be geomagnetic imprinting. Salmon are hypothesized to imprint on the specific properties of the earth's magnetic field at the mouth of their natal river system ([Lohmann, Putnam, & Lohmann 2008](#); Putnam et al. 2013). In particular, they are thought to learn the inclination angle and/or intensity of the earth's magnetic field at this location, both of which vary with latitude ([Figure 10.32](#)). Studies have shown that salmon can respond to different magnetic field intensities, and juvenile salmon will change their orientation in tanks in response to a change in the external magnetic field ([DeBose & Nevitt 2008](#)).



**FIGURE 10.32. Salmon geomagnetic navigation.** Salmon can imprint on the intensity of the earth's magnetic field ( $X_{\text{imprint}}$ ) at the mouth of their natal river system (bold line). To return to their natal site from the open ocean (O), they need to travel north (or south) toward this intensity (R arrow) and then turn east and remain along this intensity until they reach the coast. (Source: [Bracis & Anderson 2012](#))

These studies illustrate how researchers study bicoordinate navigation and reveal that a variety of animals possess such a capability. We still have much to learn about the navigational abilities of most species, including humans ([Applying the Concepts 10.3](#)).

### APPLYING THE CONCEPTS 10.3

#### Human magnetic orientation

In this chapter we've seen that many species orient using the earth's magnetic field. Is there any evidence that humans can do so too? In 1980, R. Robin Baker presented evidence that humans, after being displaced, were able to recognize their homeward direction without visual cues ([Baker 1980](#)). He conducted a series of experiments in which college students were blindfolded and then transported in a circuitous route to a location 6 to 52 km from where they had lived for at least two years (Manchester University in Great Britain). He asked each student to indicate the direction home while still blindfolded. He found that, on average, students tended to indicate the correct direction. In a second experiment, he used the same procedure but placed bar magnets on the heads of half the students and brass bars (with no magnetic properties) on the heads of the other students. Those with magnets on their heads oriented randomly, while those with brass bars tended to correctly point toward home. These experiments stimulated much interest by suggesting that the earth's magnetic field plays a role in human orientation.

suggesting that the earth's magnetic field plays a role in human orientation.

In subsequent years, however, other researchers failed to replicate Baker's findings. Studies on hundreds of subjects in the United States, Australia, and Great Britain all showed that humans do not correctly orient toward home following a blindfolded displacement ([Gould & Abel 1981](#); [Fildes, O'Loughlin, Bradshaw, & Ewens 1984](#); [Westoby & Partridge 1986](#)), casting much doubt on the ability of humans to orient using a magnetic sense.

Recent work has brought renewed attention to this question. [Connie Wang and her colleagues \(2019\)](#) found a strong, specific response in human brains to manipulations of earth-strength magnetic fields. Several other studies have revealed that in many species, the ability to detect magnetic fields depends on light-sensitive chemical reactions in the retina involving a protein called cryptochrome (CRY) (Mouristen 2018; [Wiltchko & Wiltchko 2019](#)). Interestingly, humans have a similar protein in the retina (hCRY2), further reinforcing the possibility that we may also have this ability.

### Video: Can humans sense magnetic fields?

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To investigate whether hCRY2 is sensitive to magnetic fields, Lauren Foley, Robert Gegear, and Steven Reppert conducted an experiment with fruit flies ([Foley, Gegear, & Reppert 2011](#)). Wild-type flies (with CRY) respond to magnetic fields, but only in the presence of light. Mutant flies that do not express CRY show no consistent response to magnetic fields, which indicates that magnetoreception in flies involves functional CRY. The research team created transgenic fruit flies by inserting hCRY2 into the genome of the mutant flies. They found that the transgenic flies responded to magnetic fields in a light-dependent manner, just like wild-type flies. This work suggests that human hCRY2 may have the molecular capability to be a magnetosensor (i.e., involved in magnetoreception)—a possibility that awaits further testing. ■



## CHAPTER SUMMARY AND BEYOND

Animals move from one location to another during dispersal and migration. Juveniles embarking on natal dispersal leave their place of birth to find a site for reproduction. Dispersal can benefit individuals by reducing both competition with conspecifics and the likelihood of settling nearby and mating with close kin. Reviews on dispersal behavior suggest that to more completely understand these movements, we need to focus on how the environmental context of an animal (e.g., competition, habitat quality, inbreeding risk) and the internal state of an individual (e.g., body condition, physiology) interact ([Handley & Perrin 2007](#); [Clobert et al. 2009](#)). Breeding dispersal by adults is commonly observed after a reproductive failure. Much work has focused on how individuals combine and use information about their own reproductive success, the success of others nearby, and the density of individuals in the area when deciding whether to disperse to a new site (e.g., [Citta and Lindberg 2007](#)). For a comprehensive review on the evolution of dispersal, see [Ronce \(2007\)](#).

Longer, two-way movements are known as migration and allow individuals to track changes in environmental resources. Research has focused on the regulation of migration, including hormonal control of the timing of migration ([Ramenofsky & Wingfield 2007](#); [Green & Kronforst 2019](#)) and the role of memory ([Brads & Mueller 2017](#)). Migration behavior is heritable and can evolve in a population when individuals that migrate have higher fitness than those that do not. A comparative study has examined how migration behavior evolved in New World songbirds ([Winger, Barker, & Ree 2014](#)). Animals use a variety of cues to orient in the proper direction, including the position of the sun and stars and the earth's geomagnetic field. Ongoing work continues to reveal the multiple cues animals use for orientation and navigation ([Guerra, Gegebar, & Reppert 2014](#); [Endres et al. 2016](#); [Mouritsen, Heyers, & Güntürkün 2016](#)). [Mouritsen \(2018\)](#) and [Wiltshko & Wiltshko \(2019\)](#) provide additional details about magnetoreception in animals. The study of migration is being revolutionized by the development of small geolocators that can be attached to individuals to record long-distance movements ([Reynolds & Riley 2002](#); [Stutchbury et al. 2009](#); [Hussey et al. 2015](#); [Delmore et al. 2016](#)).

## CHAPTER REVIEW

### 10.1 Dispersal reduces resource competition and inbreeding

- Dispersal is a relatively short-distance, one-way movement away from a site.
- Competition for resources promotes dispersal behavior in earthworms and water boatmen.
- Natal dispersal reduces inbreeding in great tits.

### 10.2 Reproductive success and public information affect breeding dispersal behavior

- Dragonflies exhibit a win-stay lose-shift breeding dispersal pattern.
- Kittiwake breeding dispersal is influenced by the reproductive success of other individuals in the same breeding patch.

### 10.3 Individuals migrate in response to changes in the environment

- Migration is a two-way movement from one place to another, and then back.
- Neotropical birds migrate to track fluctuations in their resources.
- Migration behavior can evolve because it is heritable.
- Competition for resources and fluctuations in environmental conditions can promote migration.
- Nonmigratory and migratory individuals can coexist in a population, but may have unequal fitness.
- In dippers, the fitness of residents is higher than the fitness of migrants.

### 10.4 Environmental cues and compass systems are used for orientation when migrating

- Animals orient the proper direction when migrating using several compass systems.
- Butterflies orient using a sun compass.
- Sea turtles orient using a magnetic and geomagnetic compass.

### 10.5 Bicoordinate navigation allows

- Displaced migrating reed warblers can

**10.5 Bicoordinate navigation allows individuals to identify their location relative to a goal**

- Displaced migrating reed warblers can adjust their direction of movement to reach their goal.
- Salmon migrate back to their natal stream using olfaction and geomagnetic imprinting.

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## CHAPTER 9

# Antipredator Behavior

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### Concepts

- 9.1 [Animals reduce predation risk by avoiding detection or taking evasive action](#)
- 9.2 [Many behaviors represent adaptive trade-offs involving predation risk](#)
- 9.3 [Living in groups can reduce predation risk](#)
- 9.4 [Some animals interact with predators to deter attack](#)

### Features

- |                               |   |
|-------------------------------|---|
| <b>Scientific Process</b>     | 9.1 <a href="#">Feeding trade-off in redshanks</a>                        |
|                               | 9.2 <a href="#">Predator harassment by California ground squirrels</a>    |
| <b>Applying the Concepts</b>  | 9.1 <a href="#">Human fear of predators</a>                               |
|                               | 9.2 <a href="#">Mitigating crop damage by manipulating predation risk</a> |
| <b>Quantitative Reasoning</b> | 9.1 <a href="#">Antipredator vigilance in yellow-bellied marmots</a>      |

A while ago, while leading a group of students on a field trip in the early spring, we heard a commotion coming from a grove of trees at the edge of a field. We could hear an American crow (*Corvus brachyrhynchos*) calling loudly, so we headed in its direction to see what was going on. We were excited to see crows as their population had been devastated by West Nile virus about a dozen years before and their numbers were increasing again. As we walked we saw more crows flying toward the trees, calling loudly. Once we got to the trees, closer inspection revealed the object of their attention—a red-tailed hawk (*Buteo jamaicensis*) was perched in the top of a tree and was surrounded by crows, all calling loudly. These hawks are normally predators of small mammals, but they will also eat birds and their offspring and so posed a threat to the crows. The crows were mobbing the predator, a form of harassment behavior that can drive it away. After a few minutes the hawk took off, with the crows in pursuit.

They surrounded the hawk as it flew and began dive-bombing it, even hitting it with their wings and beaks ([Figure](#)

[9.1](#)). The hawk circled the field twice, with several crows following closely, and then flew over a hill and out of sight—this level of harassment had succeeded and the predator left the area.



**FIGURE 9.1.** Hawk and crow. Hawk being harassed by a crow.

Predators attack and kill prey, and so selection has favored behavioral adaptations in prey, like the one we observed, that reduce the likelihood that predators will kill an individual. In this chapter, we examine how animals reduce their predation risk, that is the likelihood that they will be killed by a predator. We begin by examining ways prey can reduce the probability of being detected by a predator. We also examine behaviors that enhance survival once an individual has been attacked. Next, we focus on two common antipredator adaptations that involve modifying behavior: altering habitat use level and increasing vigilance—being alert for predators. Both involve trade-offs that affect behavior, as we will see. Next, we consider how animals reduce predation risk by living in groups. We conclude by focusing on counterintuitive behaviors that involve interactions with predators in order to deter an attack.

### Video: Ravens mobbing a hawk

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### 9.1 Animals reduce predation risk by avoiding

## 9.1 Animals reduce predation risk by avoiding detection or taking evasive action

### Learning Objectives

After reading this section, you should be able to

- explain how cryptic coloration and reduced activity levels lower detection probability by predators and
- describe how prey can avoid predators after they have been detected.

Obviously, individuals cannot be killed by a predator if predators do not detect them. As we saw in [Chapter 8](#), one common morphological adaptation is to blend into the background through **cryptic coloration**—body coloration that matches the color of the environment. Individuals can also modify their behavior to reduce risk. They might try to flee or simply lie low in order to be overlooked or even take more aggression action when attacked. Experiments have found evidence for each of these behavioral adaptations.

### FEATURED RESEARCH Predator avoidance by cryptic coloration in crabs

Karen Manríquez studied the effectiveness of cryptic coloration in the crab *Paraxanthus barbiger* ([Manríquez et al. 2008](#)). These South American crabs live and feed on the benthic substrate, or bottom, of marine coastal habitats, where they are eaten by many species of fish. The benthic habitat can consist of a uniform sandy color or a more heterogeneous mixture, thanks to small shell fragments called shell-hash. Young juveniles display color variation that ranges from brown to tan to white, with many spots and stripes ([Figure 9.2](#)). As juveniles grow, their body color changes to a more uniform light purple color. Juveniles experience much higher predation than adults, and so Manríquez and her colleagues hypothesized that this complex coloration is an adaptation to minimize detection by predators, as the juveniles' color is more cryptic on the heterogeneous shell-hash background. The team predicted that this coloration reduces predation.

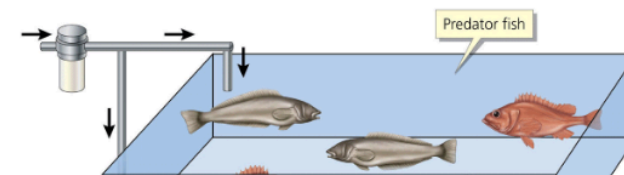


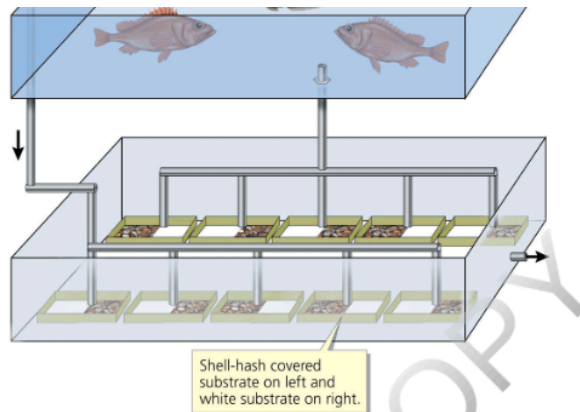
**FIGURE 9.2.** Crab coloration. Juvenile crabs have a heterogeneous coloration.

To test this prediction, the researchers tethered individual juvenile crabs (with a mean carapace width of 11 mm) to 20 cm × 20 cm ceramic tiles of different colors. One set of tiles had a uniform white surface, while the other had a heterogeneous shell-hash surface. The tether was 10 cm long, which kept the crabs on the tile for the duration of the field experiment. All the tiles were randomly placed in the ocean for a fixed period of time, and the researchers recorded the number of crabs alive at the end of the experiment. As predicted, they found very different survival rates for the crabs on the two different surfaces. Only 30% of the crabs on the white surface tiles survived, while more than 60% of the crabs on the shell-hash-colored tiles survived. From these results, the researchers concluded that juvenile crabs are indeed more cryptic when on the heterogeneous shell-hash background.

The effectiveness of cryptic coloration requires that animals live in, or use, environments that match their body color. Manríquez and colleagues next conducted a follow-up experiment to see whether crabs would select a shell-hash-colored surface over a more uniformly colored surface. They predicted that juvenile crabs would prefer the shell-hash background if given a choice, and that this preference would be stronger when predation risk was high.

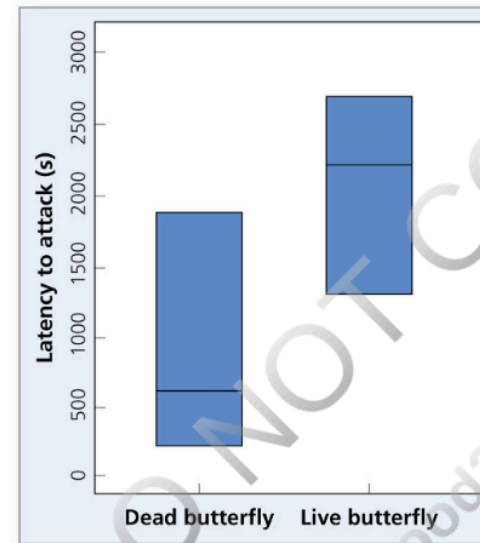
To test these predictions, they established experimental aquaria that contained ten small plastic trays (20 cm × 40 cm × 5 cm). One-half of each tray was covered by a thin layer of shell-hash, while the other was left empty and thus presented a uniformly white background ([Figure 9.3](#)). This setup gave crabs a choice of substrates to use. To manipulate predation risk, the experimenters treated half of the trays with predator odors by pumping seawater from a tank that housed several predatory fish and the other half with seawater that contained no predator odors. In each test aquarium, nine crabs were placed in the center of each tray, and the researchers recorded the proportion of these crabs on each substrate after three hours. To examine how crabs of different size would respond to these manipulations, they tested small crabs (< 10 mm in length) in one set of experiments and larger crabs (25–30 mm) in another.





**FIGURE 9.3. Crab experimental design.** Either plain water or water with fish odor could be pumped into the experimental arena, where crabs had the choice of two substrates: plain white or shell-hash covered. (Source: [Manríquez et al. 2008](#))

Of the birds that attacked at least one butterfly, significantly more (22 out of 24) attacked the dead butterfly first, and so the latency to attack differed significantly ([Figure 9.11](#)). There were a total of 158 visits to the live butterfly, and it responded with a startle display 75% of the time. In 80% of the bird visits that elicited a startle display, the great tit either quickly flew away or hopped back; the birds appeared to be startled and wary to attack the live butterfly. Only three live butterflies were killed during the experiment, suggesting an important antipredator function of the wing-flick startle display by swallowtail butterflies. Additional work is needed to determine why this behavior is such a deterrent to great tits.



**FIGURE 9.11. Latency to attack.** Median (black line) latency to attack live and dead butterflies. Each box represents the middle 50% of the data range.

Each of these examples illustrates how animals either reduce detection by predators or increase survival once attacked. Next, we examine behavioral trade-offs that reduce predation risk but come at the cost of a reduction in other behaviors.

## 9.2 Many behaviors represent adaptive trade-offs involving predation risk

### Learning Objectives

After reading this section, you should be able to



After reading this section, you should be able to

- explain how vigilance behavior affects predation risk,
- compare the trade-off between vigilance and feeding behavior,
- analyze the trade-off between predation risk and the quality of feeding sites, and
- cite examples of how predation risk can influence reproductive behavior.

A world without predators would allow animals to concentrate their behavior on activities that maximize their fitness, perhaps by increasing time spent searching for mates. In that light, the existence of predators represents a cost to animals: they modify their behavior to reduce the probability that they will be killed, as we saw previously. Sacrificing one activity for another is known as a behavioral trade-off. Such trade-offs are widespread, as we see next.

## Increased vigilance decreases feeding time

A widespread trade-off involves **vigilance behavior**, or scanning for predators (Figure 9.12). When many animals search for food, they often lower their head as they focus their attention on finding food items on or in the ground. This head-down position usually results in a reduced visual scanning range. Vegetation, such as grasses or other plants, can also increase the obstruction of an animal's scanning range. Consequently, when an individual has its head down, it experiences a higher risk of predation. To counter this risk, individuals typically raise their head periodically to scan their surroundings for predators. Such vigilance behavior is ubiquitous: you can observe it by watching squirrels, birds, or deer feeding on a lawn.



**FIGURE 9.12. Vigilance.** Flamingos (*Phoenicopterus roseus*) in the foreground have their head up, engaged in vigilance behavior, while those in the background are feeding with their heads down.

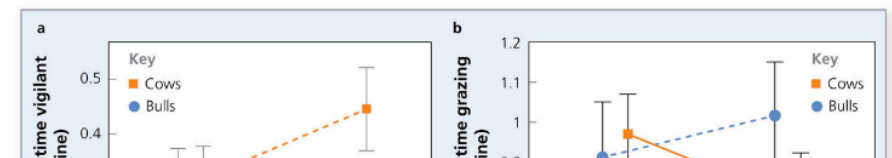
Because an individual usually cannot simultaneously search the ground for food and scan effectively for predators, vigilance involves a behavioral trade-off. In theory, doubling the amount of time spent scanning will halve an individual's time spent feeding. This will result in both a decrease in the probability of being killed by a predator and an increase in the individual's risk of starvation (McNamara & Houston 1987), illustrating the trade-off. We can predict that animals will adjust their vigilance based on the level of risk in the environment: as predation risk increases, so should vigilance (Brown 1999).

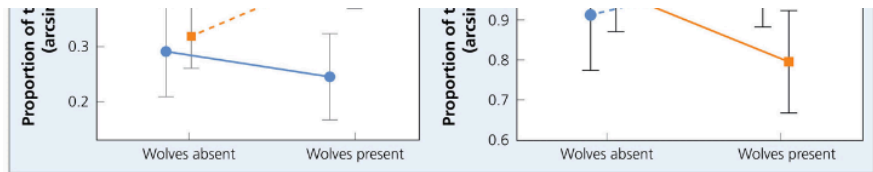
## FEATURED RESEARCH Vigilance and predation risk in elk

One test of this prediction involves elk (*Cervus canadensis*) in four large drainages near Yellowstone National Park. For much of the twentieth century, elk lived in an environment free of wolf (*Canis lupus*) predators. In the 1990s wolves were reintroduced to portions of the park, creating areas with and without wolf predators. John Winnie and Scott Creel examined how elk behavior was affected by the presence of this predator (Winnie & Creel 2007).

Over a three-year period, they recorded the behavior of elk and the presence of wolves each winter. Every two weeks, the researchers used instantaneous scan sampling to record the behavior of all members of elk herds in different drainages: they recorded the proportion of time spent feeding, moving, bedded, or vigilant. For each herd, the researchers classified whether wolves were or were not present in the drainage. To determine the presence of wolves, they walked fixed transect routes, looking for signs such as fresh kills, scat, or tracks. These data were supplemented with information from a few radio-collared individuals.

They collected data on 88 elk herds and a total of 11,287 instantaneous scan samples. Most elk herds were small (mean of approximately 14 individuals) and only a few contained both cows and bulls. Elk spent 61% of their time foraging and almost 16% of their time vigilant. The presence of wolves in a drainage had a strong effect on the behavior of female elk. Females spent significantly more time vigilant and less time feeding when wolves were nearby; in contrast, male behavior was largely unaffected by the presence of wolves (Figure 9.13). The researchers suggest two reasons for these results. First, bulls are about 30% larger than cows and thus may represent a more dangerous challenge to wolf predators than cows. Second, reproductive success for males largely depends on maintaining high body mass, and so males have more to lose by reducing feeding time, even if the consequence is higher predation risk when wolves are nearby.





**FIGURE 9.13. Elk behavior.** Mean ( $\pm$  SE) proportion of time (a) vigilant and (b) grazing by cows (females - orange) and bulls (males - blue) in response to the presence or absence of wolves. (Source: [Winnie & Creel 2007](#))

## Rich but risky

In most habitats, there are risky and safe locations. In addition, in any environment, some habitat patches contain abundant food, and others contain less food. Let's call patches with abundant food *rich patches* and those with less food *poor patches*. Animals obviously should prefer to feed in rich patches because they can obtain higher energy intake rates there. However, many rich patches are often found in places with higher numbers of predators or higher predator attack rates. That means that in order to feed in a rich patch, individuals must be willing to subject themselves to higher predation risk. We can therefore ask two research questions: How often will animals be willing to accept higher predation risk in order to feed in richer patches, and what factors might favor animals feeding in richer but riskier patches? The next example illustrates how foragers balance predation risk and food acquisition when rich but risky places to feed are available.

## FEATURED RESEARCH Environmental conditions and predation risk in foraging redshanks

Redshanks (*Tringa totanus*) are medium-sized (approximately 28 cm in length) wading birds in the sandpiper family that live throughout Eurasia. They have a long, straight bill, which they use to find insects, earthworms, mollusks, and crustaceans that are buried in the soil. Redshanks can be found feeding in a variety of habitats, including salt marshes and mudflats near the coast.

Mai Yasué and her colleagues ([Yasué, Quinn, & Cresswell 2003](#)) examined a trade-off between predation risk and foraging in a population of these birds ([Scientific Process 9.1](#)). In particular, they studied how weather conditions and predation risk affected daily feeding decisions during the winter in Scotland. The main predators in this area are sparrowhawks (*Accipiter nisus*). The researchers first observed that predators were much more common in the salt marsh habitat than the mudflat habitat, with 20 times more predator attacks on redshanks occurring when they fed in the former compared to the latter. Yasué and colleagues concluded that the salt marsh habitat was riskier for a redshank than the mudflat habitat. Given this level of risk, one might conclude that redshanks should always feed in the mudflat habitat if they want to avoid predators. However, Yasué and colleagues observed that on some winter days, redshanks seemed to feed more often in the riskier salt marsh habitat. Why?

### Video: Redshank feeding

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### Video: Redshank feeding

### Video: Sparrowhawk attacking redshank

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### SCIENTIFIC PROCESS 9.1

#### Feeding trade-off in redshanks

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Research  
Question:

*Why do redshanks sometimes feed in the riskier salt marsh habitat instead of the safer mudflat habitat?*

#### Hypothesis:

Energetic requirements and predation risk affect feeding behavior.

#### Prediction (1):

The salt marsh habitat contains more food than the mudflat habitat.

#### Prediction (2):

As the temperature drops, redshanks will feed more often in the salt marsh habitat to meet their energy needs.

#### Methods (1):

The researchers:

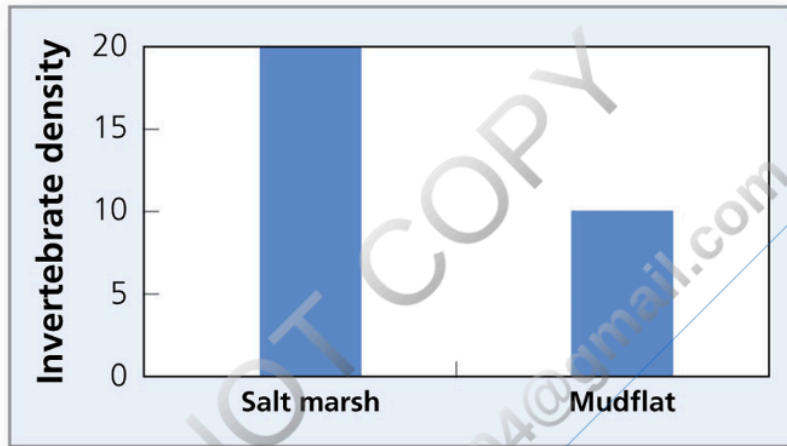
- Collected samples from 2 to 4 cm (depth of bill probe) of the substrate in small plots ( $n = 47$ ) and then counted and identified all invertebrates found there

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### Results (1):

There were twice as many invertebrates per sample in the salt marsh habitat as there were in the mudflat habitat.



**FIGURE 1. Food abundance.** The salt marsh habitat contains more invertebrate food than the mudflat habitat. (Source: [Yasue, Quinn, & Cresswell 2003](#))

### Conclusions (1):

There is twice as much food available for redshanks in the salt marsh habitat as there is in the mudflat habitat.

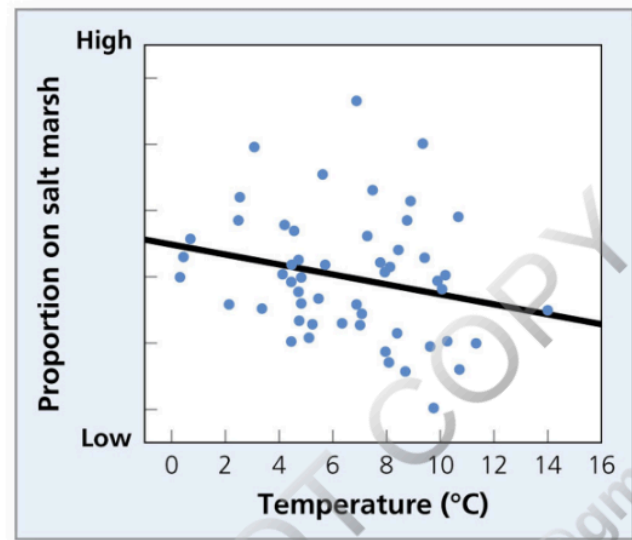
### Methods (2):

The researchers:

- Recorded the number of redshanks feeding in the salt marsh within three hours of low and high tide and the ambient temperature over the course of 91 days

### Results (2):

As ambient temperature decreased, more redshanks fed in the salt marsh habitat.



**FIGURE 2. Redshank behavior.** More redshanks fed in the salt marsh habitat when the temperature was low. (Source: [Yasue, Quinn, & Cresswell 2003](#))

### Conclusions (2):

When it is cold, redshanks feed in the risky salt marsh habitat because it contains more food than the mudflat habitat. Feeding there should thus result in higher energy intake rates to meet these individuals' energetic requirements.

### Evaluate

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Describe the adaptive trade-off involving predation risk in this study.

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Birds, like mammals, are endotherms. They generate their own internal body heat, and when it is cold outside, their body temperature is much higher than the ambient temperature. To maintain their high internal body temperature, birds (and mammals) need to consume more food as the temperature drops. This characteristic led Yasué and colleagues to hypothesize that energetic requirements and predation risk affect redshank feeding behavior. That is, when the outside temperature is low, birds cannot find sufficient food by feeding only in the safer mudflat habitat. This hypothesis predicted that the salt marsh habitat contains more food than the mudflat habitat, and that ambient temperature affects where redshanks will feed. On the coldest days of the year, redshanks will prefer to feed in salt marsh habitats.

To test their first prediction, the researchers measured the amount of food available in both the salt marsh and the mudflat habitats every two weeks over the course of the winter. They found that there were roughly twice as many invertebrates in each sample from the salt marsh habitat as there were in those from the mudflat habitat throughout the winter, which supported their first prediction. To test the second prediction, they recorded the number of redshanks that fed in each of the two habitats each day over the course of the winter, as well as the temperature on those observation days. As predicted, environmental temperature was strongly correlated with the behavior of the birds: the number of redshanks feeding in the salt marsh habitat increased significantly as the temperature declined. Thus, on colder days, most birds fed predominately in salt marshes, where they could obtain more food, but at a cost of suffering higher predator attack rates. From these data, the researchers concluded that the behavior of redshanks was consistent with the hypothesis that individuals trade off higher predation risk in the salt marsh for the higher energy intake rates they obtain there.

This type of foraging–predation risk trade-off is widespread across taxa. Invertebrates also behave in ways that trade off predation risk and habitat use, as we see next.

## FEATURED RESEARCH Mating and refuge use in fiddler crabs

Fiddler crabs (*Uca mjoebergi*) live in intertidal habitats and feed on the surface of the sand during low tide. The species gets its name from the morphology of the males, which possess a single large claw that they wave back and forth in a sexual display to attract females (Figure 9.14). Individuals construct and live in burrows in the sand, which provide a safe refuge from bird, mammal, and reptile predators. To feed or attract mates, crabs need to be active aboveground, but they will quickly retreat to their burrow in response to a predator attack.



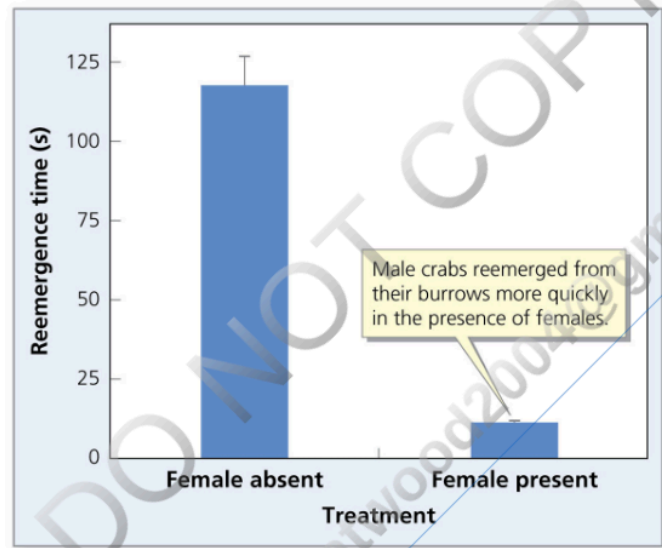
**FIGURE 9.14. Fiddler crabs.** Males use burrows in the sand for protection from predators. They wave their large claw to attract females.

Leeann Reaney examined how predators and mating opportunities affect refuge use by male fiddler crabs (Reaney 2007). The benefit of refuge use is that it provides protection from predators. The cost is that a male inside a burrow cannot court a female. Reaney hypothesized that male crabs would adjust their refuge-use behavior based on its costs and benefits. Specifically, she predicted that males would emerge from their refuges more quickly after an attack (and thus expose themselves to risk) if potential mating opportunities were available aboveground.

To test this prediction, Reaney created 30 small plots (35 cm × 35 cm) in a coastal intertidal mudflat in Darwin, Australia. Each plot contained several males and their burrows. In 15 of these plots, she tethered a single, sexually receptive female by gluing a thin piece of string onto its carapace and attaching it to a nail buried in the sand. The other 15 plots served as controls and did not contain a tethered female. Reaney first waited for all the males in a plot to become active aboveground. She then flew an artificial model of a bird predator over the plot and recorded

how long the males stayed in their burrows after the “attack.” She averaged the measurements for all males within each plot and compared the average values for males in each treatment.

Reaney found that all males in the control plots retreated into their burrows and stayed underground for about 120 seconds. In contrast, in the plots with a receptive female, 12% of males did not retreat into their burrow during the attack. Those males that did flee into their burrow reemerged in less than 15 seconds (Figure 9.15). From these results, Reaney concluded that males adaptively adjust their refuge use based on its benefits and costs. Males trade off the safety of the burrow for increased mating opportunities when receptive females are present. When presented with no mating opportunities, males use their burrows much more.



**FIGURE 9.15. Male reemergence times.** Mean (+ SE) reemergence times of courting male fiddler crabs after a predator attack in plots with and without females present. (Source: [Reaney 2007](#))

**Video: Male fiddler crabs waving their claws**

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**FEATURED RESEARCH Perceived predation risk affects reproductive behavior in sparrows**

Predation risk not only affects mating behavior as we just saw in fiddler crabs, but it can also affect reproduction itself, through multiple behavioral trade-offs. One example comes from the work of Liana Zanette, Aija While, Marek Allen, and Michael Clinchy on song sparrows (*Melospiza melodia*) nesting in British Columbia, Canada ([Zanette et al. 2011](#)). Song sparrows nest in shrubs and can lose half their offspring to predators such as raccoons (*Procyon lotor*), crows, and hawks and so predators clearly affect the population. Zanette and her colleagues examined whether changes in perceived predation risk could also affect song sparrow life history.

**Video: The researcher reviews the experimental design and result**

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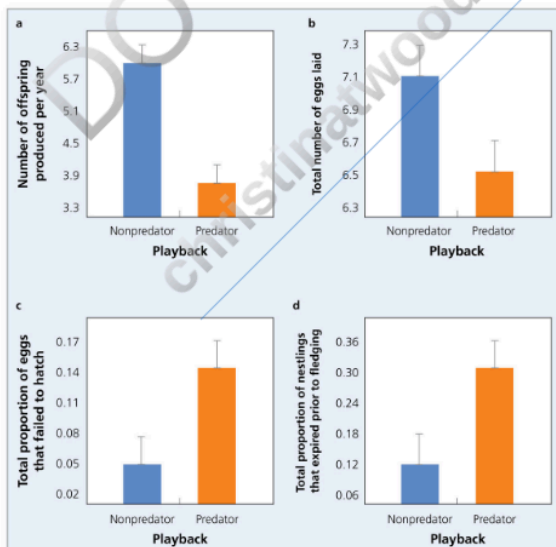
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In a unique experiment, the researchers eliminated direct predation on nests by protecting them with both electric fencing and seine netting. This prevented the larger predators from accessing nests without disrupting sparrow behavior. They then continuously recorded the breeding activities of 24 females over the course of one breeding season. Females were subjected to one of two treatments that manipulated their perceived predation risk. For half the females, the researchers played vocalizations of common predators every few minutes for four consecutive days followed by four days of silence, repeated over the breeding season. For control females, the researchers played vocalizations in a similar manner using nonthreatening species such as seals, loons, and hummingbirds.

All females produced two broods over the season but differed significantly in their reproductive activities. Individuals exposed to predator vocalizations nested in denser vegetation, laid fewer eggs and had fewer offspring, and had a greater proportion of their nestlings die compared to control females (Figure 9.16). Higher perceived predation risk resulted in a 40% decrease in the number of offspring produced. These results indicate that perceived predation risk alone is enough to affect reproductive behavior.



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## 9.3 Living in groups can reduce predation risk

### Learning Objectives

After reading this section, you should be able to

- differentiate between the dilution effect and the selfish herd, and
- predict how group size should affect scanning rates.

Many animals live in **social groups**, meaning they live near and interact with other individuals. One important benefit of this behavior for social animals is that living in groups can reduce predation risk. In Chapter 15, we examine social behavior in more detail. Here, we focus on some of the ways that social animals experience lower levels of predation risk than solitary individuals.

### FEATURED RESEARCH The dilution effect and killifish

Suppose a predator attacks a pair of animals and kills one. For each prey, there was a one-half probability that it would be the one killed. If there had been ten prey, there would have been only a one-tenth probability that any one individual would be killed. In a group of 100 individuals, that probability would fall to one-hundredth. The probability of any one individual's dying is diluted by the presence of others, known as the **dilution effect** (Foster & Treherne 1981).

In the dilution effect, there is a  $1/N$  probability of dying when a predator makes a single kill in a group of  $N$  individuals. As group size  $N$  increases, the probability that any single individual dies decreases. Clearly, this size increase can greatly reduce an individual's probability of dying as a result of a predator attack, especially in a group of hundreds or thousands of individuals. The only behavior required for the dilution effect to occur is for an individual to join others in a group.

D. J. Hoare and colleagues (Hoare et al. 2004) examined the dilution effect in a simple laboratory experiment using banded killifish (*Fundulus diaphanus*). They predicted that fish should prefer to associate with larger groups rather than smaller groups, particularly when predation risk is high. Banded killifish are small (< 10 cm standard length) freshwater fish that live in eastern North America. These fish tend to move in shoals and can use chemical cues to perceive predation risk. The researchers compared the sizes of groups that killifish formed in a high-predation risk treatment with the group sizes formed in a control treatment.

Experiments were conducted in a large tank (100 cm × 100 cm × 15 cm). To simulate high predation risk, the researchers added a diluted concentration of killifish skin extract to the tank. Many species of fish respond to the crushed skin extract of conspecifics, presumably because it indicates the presence of a predator that has made a

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kill nearby. In the control treatment, only water was added to the aquarium. For each trial, ten killifish were placed in the experimental tank and allowed to acclimate overnight. The next day, skin extract (treatment) or water (control) was added to the tank, and a 60-minute trial was recorded. From the recordings, the researchers recorded shoal size every 30 seconds. Individuals were considered to be in the same shoal if they were within four body lengths of one another.

The results of the experiment were clear: median shoal size in the control was just two fish, with most fish swimming alone in the aquarium, while median shoal size in the high-predation risk treatment was ten fish, the maximum group size. From these results, Hoare and colleagues concluded that banded killifish prefer to associate with more individuals when predation risk is high, as predicted by the dilution effect.

## The selfish herd and vigilance behavior

A second way social groups can lower predation risk is for individuals to stay near the group's center. The **selfish herd hypothesis** (Hamilton 1971) assumes that a predator is more likely to kill a member on the outside of a group because it will encounter outside individuals first (Figure 9.17). Individuals can therefore lower their predation risk by placing others between themselves and an approaching predator. In contrast to the dilution effect, the selfish herd hypothesis requires individuals to continually adjust their position in a group.

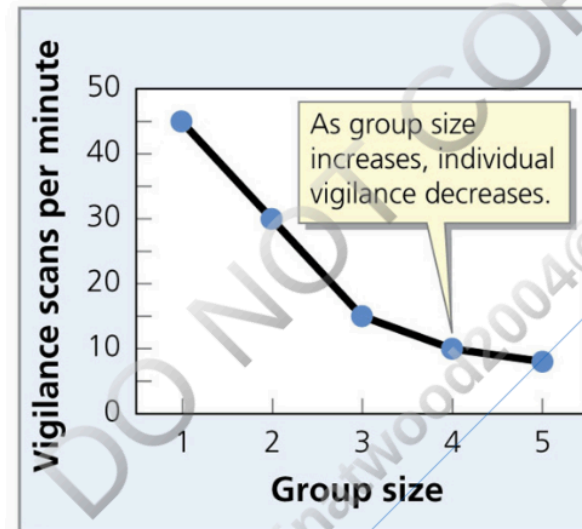


**FIGURE 9.17. Selfish herd.** Rock doves (*Columba livia*) on the exterior of the flock are more likely to be killed by a predator than are individuals in the center.

A third antipredator benefit of associating with others involves vigilance behavior. In social groups, more

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individuals can be vigilant, and hence "more eyes" can observe potential predators. Many researchers have documented a common pattern known as the **group size effect** (Pulliam 1973), in which the vigilance behavior of each individual decreases as the number of individuals in its group increases (Figure 9.18). The group size effect has been observed in a wide variety of birds, mammals, and even fish, and it is thought to result from two factors. First, as group size increases, each individual is safer because of the dilution effect, and so can reduce its level of vigilance. Second, as group size increases, each individual can afford to scan less frequently because more individuals are scanning. Therefore, the collective vigilance of the entire group can remain high even though each individual scans less often. If one individual in the group sees a predator, it will quickly flee to protective cover. That motion alerts other group members to the imminent danger so that they too can respond appropriately. Next we examine a study of doves that investigated both the group size effect and the selfish herd hypothesis.



**FIGURE 9.18. Group size and vigilance.** The relationship between group size and individual vigilance.

## FEATURED RESEARCH Group size effect and the selfish herd hypothesis in doves

Scaled doves (*Columbina squammata*) are small birds that are widely distributed throughout Latin America (Figure 9.19). Raphael Dias studied dove scanning and foraging behavior on the University of Brasília campus (Dias 2006). He investigated two research questions. First, he wondered whether scaled doves exhibit the group size effect. If so, he predicted that they should exhibit reduced scanning rates as their group size increases.

Second, he examined whether doves at the edge of a flock are exposed to higher predation risk, as assumed in the selfish herd hypothesis. If so, he predicted they should exhibit higher scanning rates than individuals at the center

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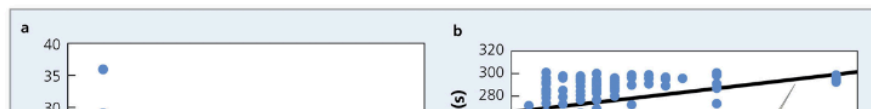
of a flock.



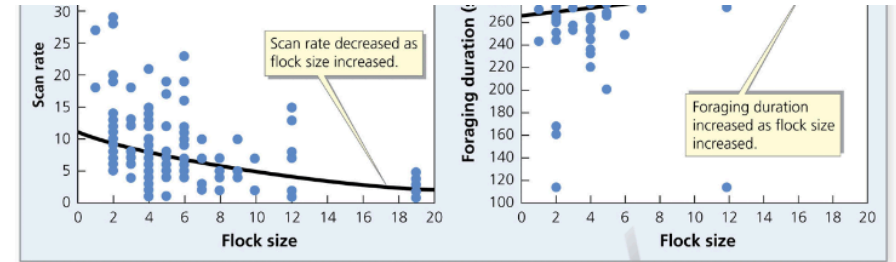
**FIGURE 9.19. Scaled dove.** These small doves are common throughout Latin America.

Dias studied wild flocks all over the campus for two months. When he found a flock of feeding birds, he recorded the group size and then selected one focal animal. He recorded the location of the focal bird in the flock (central or edge position), its scan rate (the number of times it lifted its head to scan the environment over a five-minute period), scan durations, and the total amount of time it spent feeding. He also made note of any position shifts in the focal bird (i.e., any change from a central to an edge position or vice versa). He then moved to a different location on campus to find another flock. In total, he observed 150 flocks that varied in size from one to 19 individuals.

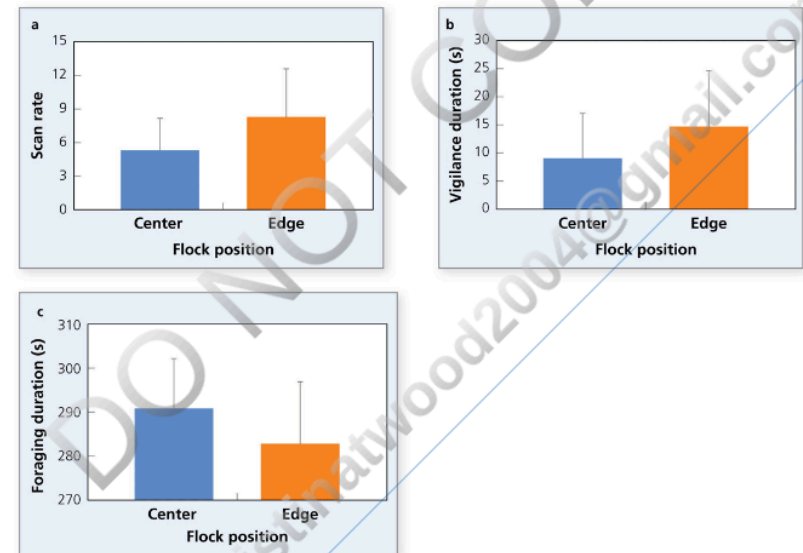
Dias found that individual vigilance behavior decreased significantly as group size increased, indicating that these doves did indeed exhibit the group size effect. In addition, the feeding time of individuals increased as group size increased (Figure 9.20). Furthermore, individuals in the center of a flock behaved differently than did individuals at the edge. Birds in the center exhibited lower scan rates and had higher feeding rates than individuals at the edge of a flock (Figure 9.21). When position shifts did occur, individuals more often moved from the edge of the flock to the center—that is, they exhibited behavior consistent with the selfish herd hypothesis.



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**FIGURE 9.20. Group size effect in doves.** The relationship between (a) scan rates (scans/5 min) and (b) foraging duration for different flock sizes. (Source: Dias 2006)



**FIGURE 9.21. Center and edge dove data.** Mean (+ SE) (a) scan rate (scans/5 min), (b) vigilance, and (c) foraging duration for birds in the center and at the edge of flocks. Doves in the center scanned less, were less vigilant, and also foraged more than doves on the edge. (Source: Dias 2006)

Dias concluded that doves exhibit a trade-off between scanning for predators and feeding: scan rate declines and feeding time increases strongly with group size. In addition, the data support an important assumption behind the selfish herd hypothesis: individuals at the edge of a group appear to experience a higher threat of predation than do individuals near the center of a group.

If there are benefits to being near the center of a group (lower predation risk, higher feeding times), why don't all birds try to move to the center? Dias suggests that a dominance hierarchy maintains group position: dominant

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individuals most likely can maintain their central position, while subordinate individuals are forced to stay in more peripheral positions (see [Chapter 11](#)).

These examples illustrate how individuals in groups can benefit from reduced predation risk. In all these examples, individuals behave to avoid predators. In the last section, we examine how selection can favor a counterintuitive antipredator behavior: the direct interaction of individuals with predators.

Dias concluded that doves exhibit a trade-off between scanning for predators and feeding: scan rate declines and feeding time increases strongly with group size. In addition, the data support an important assumption behind the selfish herd hypothesis: individuals at the edge of a group appear to experience a higher threat of predation than do individuals near the center of a group.

If there are benefits to being near to the center of a group (lower predation risk, higher feeding times), why don't all birds try to move to the center? Dias suggests that a dominance hierarchy maintains group position: dominant individuals most likely can maintain their central position, while subordinate individuals are forced to stay in more peripheral positions (see [Chapter 11](#)).

These examples illustrate how individuals in groups can benefit from reduced predation risk. In all these examples, individuals behave to avoid predators. In the last section, we examine how selection can favor a counterintuitive antipredator behavior: the direct interaction of individuals with predators.

## 9.4 Some animals interact with predators to deter attack

### Learning Objectives

After reading this section, you should be able to

- explain predator harassment,
- compare the pursuit deterrent and alarm signal hypotheses, and
- describe how advertisement behavior can reduce predation risk.

Predators cannot be entirely avoided. When an encounter occurs, many individuals flee to a safe location, but in some situations, a potential victim does *not* flee. Instead, it actively interacts with a predator. Recall from the beginning of the chapter that when songbirds observe a hawk, they will often engage in **predator harassment**, behavior that involves rapid movement such as diving at or around a predator and is often coupled with loud vocalizations. Some species, like chimpanzees, will throw objects at a predator. Others, like ground squirrels and kangaroo rats, will kick dirt at a predator. The harassment of a predator by more than one individual is known as **mobbing behavior**.

On the surface, predator harassment behavior appears to increase the likelihood that an individual will be killed, because it means direct interaction with a predator within a short distance. So why would an individual harass a predator? One possible answer is that such behavior can cause a predator to become more defensive, reducing its likelihood of attack. In addition, harassment could simply cause the predator to move away. Still other species will engage in behaviors that appear to enhance or “advertise” their presence to a predator. Advertisement behavior might benefit an individual by conveying to a predator that it has lost the element of surprise. Let's see how researchers have tested each of these explanations.

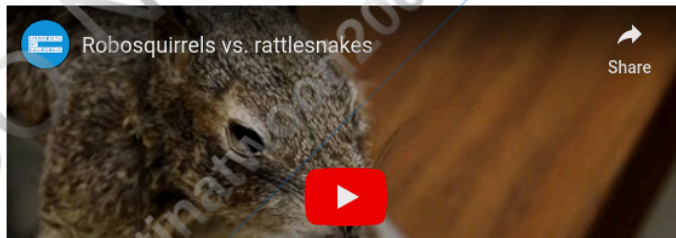
## FEATURED RESEARCH Predator harassment in ground squirrels

Aaron Rundus and colleagues examined interactions between California ground squirrels (*Spermophilus beecheyi*) and rattlesnake predators. Adult squirrels have evolved several behavioral and physiological adaptations to defend their pups from predation by Pacific rattlesnakes (*Crotalus oreganus*). Adults are not susceptible to rattlesnake venom, but pups are vulnerable, and so adults often confront and harass snakes to deter their hunting behavior (Rundus et al. 2007). Squirrels will harass snakes by making rapid movements, engaging in vigorous tail-flagging (a rapid wagging of the tail), and even kicking dirt and rocks at them. Rattlesnakes are pit vipers and have heat-sensitive pit organs that can perceive infrared radiation (Chapter 5). Other snakes, such as gopher snakes, are insensitive to infrared radiation. Rundus and colleagues investigated whether ground squirrels' harassment of rattlesnakes also had an infrared component and whether such harassment caused snakes to become more defensive (Scientific Process 9.2).

### Video: Researchers describe robot squirrels and rattlesnakes experiments

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Video: Researchers describe robot squirrels and rattlesnakes experiments



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### SCIENTIFIC PROCESS 9.2

#### Predator harassment by California ground squirrels

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Research Question: How do California ground squirrels harass rattlesnakes?

### Hypothesis:

Ground squirrels use an infrared signal during rattlesnake harassment by increasing blood flow to their extremities.

### Prediction:

When attacked by a rattlesnake, a ground squirrel will shunt more blood to its tail than it will when being attacked by a gopher snake (*Pituophis melanoleucus*).

### Methods:

The researchers:

- Conducted four types of randomly ordered trials using 12 adult female squirrels: (1) a baseline trial with no stimuli, (2) a control trial with a conspecific (squirrel) stimulus, (3) an experimental trial with a northern Pacific rattlesnake stimulus, and (4) an experimental trial with a gopher snake stimulus
- Placed a squirrel's home cage next to the opening of the test chamber. Trials began after the squirrel engaged the stimulus animal in the test chamber. Baseline and control trials

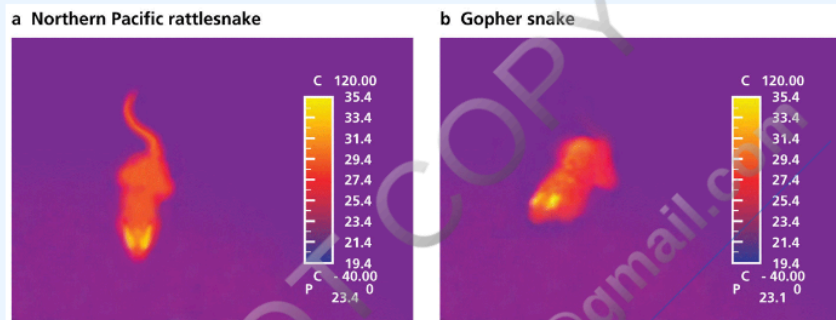
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were compared to experimental trials. Ten-minute trials were spaced two days apart.

- Used infrared video to collect data on squirrel body and tail temperature

## Results:

The temperature of a ground squirrel's tail was, on average, 2°C higher when the squirrel harassed a rattlesnake than when it harassed a gopher snake.



**FIGURE 1. Ground squirrel tail temperature.** Note the squirrel's higher tail temperature (indicated by a red tail in the infrared image) when harassing (a) a rattlesnake compared with (b) a gopher snake. (Source: Rundus et al. 2007)

## Conclusion:

California ground squirrels include an infrared component in their harassment of rattlesnakes, presumably by increasing blood flow to the tail, which results in a slowing of the snake attack.

## Evaluate

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Why don't ground squirrels increase their body temperature rather than just their tail temperature as an antipredator signal?

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The researchers staged encounters between adult ground squirrels and different stimuli (treatments). One stimulus was an adult Pacific rattlesnake, another was an adult gopher snake, and a third was a control (another ground squirrel). Each stimulus was housed in a wire mesh cage that prevented direct contact but allowed the passage of visual, auditory, olfactory, and infrared information. All trials were recorded with an infrared-sensitive video camera, which allowed the researchers to quantify the heat given off by the ground squirrel from different parts of its body during an encounter. The researchers also measured the temperature of both the bodies and the tails of the ground squirrels.

During encounters with both species of snakes, all ground squirrels exhibited harassment behavior, particularly tail flagging. No harassment behavior was observed in interactions with another ground squirrel. Interestingly, analysis of the recordings also revealed that the ground squirrel tail temperature was much higher during encounters with the rattlesnake compared to encounters with the gopher snake. Ground squirrels appear to add an infrared component to their harassment behavior, but only when they interact with rattlesnakes that can detect such signals.

How effective is this harassment behavior? Does it indeed put predators on the defensive? To determine how the infrared signal might affect rattlesnakes, another experiment used robotic ground squirrel models based on lifelike taxidermy mounts. The researchers could manipulate the models to exhibit tail-flagging behavior and could alter the temperature of the tail. Rundus and colleagues then trained adult Pacific rattlesnakes to actively search for food in a simulated ground squirrel burrow they created in the laboratory. This setup required the snakes to travel over 1 m to enter the burrow. After the snakes were trained, a model squirrel was placed next to the burrow entrance, and a snake was introduced into the experimental arena.

The researchers exposed each snake to two treatments. In one, the model ground squirrel tail-flagged with a cold tail (thus producing no infrared signal). In the other, the model tail-flagged with a warm tail (thus producing an infrared signal in the tail). The team found that when a snake interacted with a model that gave off an infrared signal, it exhibited more defensive behaviors (e.g., defensive coiling) and moved less (reduced search behavior). This experiment, examining a proximate antipredator mechanism, shows that adding an infrared component to predator harassment behavior is an effective strategy for hindering a snake predator. Why do rattlesnakes exhibit more defensive behaviors in response to the infrared signal? Squirrels often combine tail flagging with substrate throwing, and so snakes may have anticipated additional harassment. Rattlesnakes also often hunt at dusk, when it might be difficult to observe the tail-flagging behavior. The addition of the infrared signal by squirrels may enhance tail-flagging behavior in such low-light conditions. However, this hypothesis remains to be tested.

## Pursuit deterrence and alarm signal hypotheses

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Predator harassment is one antipredator behavior exhibited by animals that have spotted a predator. Another involves behaving in a manner that appears to make an individual more obvious to potential predators. For example, after spotting a predator, Thomson's gazelles (*Eudorcas thomsoni*) and impala (*Aepyceros melampus*) will stot, a behavior that resembles pogo stick-hopping as they move forward, while zebra-tailed lizards (*Callisaurus draconoides*) will raise their long black-and-white tail and wag it back and forth (Figure 9.22). You may have seen such "advertisement" behavior if you have ever startled a white-tailed deer (*Odocoileus virginianus*) while walking in the woods. Many times, when deer spot a predator (including humans), they lift and wag their tail, revealing the white underside, as they move a short distance away.

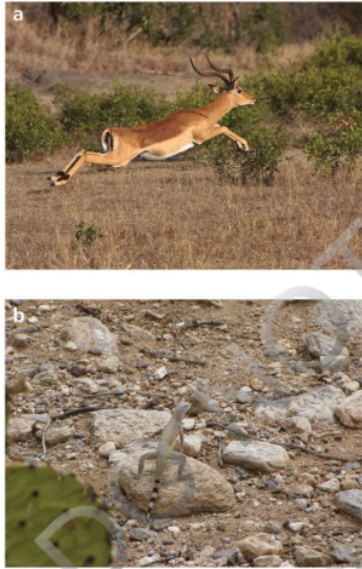


FIGURE 9.22. Advertisement behavior. (a) Impala stotting. (b) Zebra-tailed lizard.

At first, these behaviors seem to be at odds with behaving to minimize exposure to predators. Why would a prey advertise itself to a predator? One possible answer is the **pursuit-deterrence hypothesis**: advertisement behavior informs the predator that it has been detected and so pursuit is not likely to be successful.

disappearance hypothesis states that the bright white of the underside of the tail gives the predator an easily observed target. They predicted that the sudden disappearance of this target against the dark background of dense woods means that the predator will have trouble locating its prey and will give up its attack. At the conclusion of their study, Caro and colleagues could reject the alarm signal hypothesis. They also found support for the pursuit-deterrence hypothesis and formulated a new hypothesis for tail flagging—it functions to confuse a predator by providing a target that disappears when a deer drops its tail after running into dense vegetation. Additional tests of these hypotheses are needed using real predator–deer interactions.

## CHAPTER REVIEW

### 9.1 Animals reduce predation risk by avoiding detection or taking evasive action

- The cryptic coloration of juvenile crabs is an adaptation to minimize detection by predators.
- Whiptail lizards reduce their activity level in the presence of predators to reduce detection.
- Caterpillars and butterflies use aggressive or startle antipredator behaviors when attacked.

### 9.2 Many behaviors represent adaptive trade-offs involving predation risk

- There is often a trade-off between antipredator vigilance and feeding behavior.
- Female, but not male, elk increased vigilance and decreased foraging in the presence of wolf predators.
- Redshanks forage in high-quality, rich food patches in risky locations on colder days to obtain more food.
- Male fiddler crabs adjust reproductive behaviors in response to variation in predation risk.
- Female song sparrows decrease their reproductive activities in response to an increase in perceived predation risk.

### 9.3 Living in groups can reduce predation risk

- Predation risk for individuals declines as group size increases, even when individual vigilance levels decline as group size increases.
- Killifish prefer larger schools as predation risk increases.
- Scaled doves display selfish herd behavior as individuals prefer to forage in the center of the group.

### 9.4 Some animals interact with predators to deter attack

- Predator harassment, such as in ground squirrels, and mobbing behavior can reduce predation risk.
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## CHAPTER 8

# Foraging Behavior

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### Concepts

- 8.1 [Animals find food using a variety of sensory modalities](#)
- 8.2 [Visual predators find cryptic prey more effectively by learning a search image](#)
- 8.3 [The optimal diet model predicts the food types an animal should include in its diet](#)
- 8.4 [The optimal patch-use model predicts how long a forager should exploit a food patch](#)
- 8.5 [Some animals obtain food from the discoveries of others](#)

### Features

#### Scientific Process

- 8.1 [Prey detection by gray mouse lemurs](#)
- 8.2 [Cryptic prey reduces predator efficiency](#)
- 8.3 [Patch use by fruit bats](#)

#### Applying the Concepts

- 8.1 [Human patch-leaving decisions](#)
- 8.2 [GUDs and conservation](#)

#### Toolbox

- 8.1 [Mathematical solution to the optimal diet model](#)

#### Quantitative Reasoning

- 8.1 [Foraging in different habitats](#)

We are fortunate to live near a large butterfly conservatory. The conservatory is designed to mimic the hot, humid, tropical environment of many butterfly species, making it a fun place to visit on a cold winter day! There are approximately two thousand butterflies from up to 80 species living there, foraging, resting, and sometimes even mating on approximately 150 species of plants.

We often take students to the conservatory to study butterfly foraging behavior. Our students frequently observe

we often take students to the conservatory to study butterfly foraging behavior. Our students frequently observe that individual butterflies will visit many different flowers while foraging ([Figure 8.1](#)). They also often report much variation in the amount of time an individual spends feeding on one flower: an individual sometimes spends a short time at one flower and then a longer amount of time at a different flower even when both are the same species. Other observations indicate that individuals vary greatly in how long they spend searching for a new flower to land on. What are the butterflies doing? You will find the answer in this chapter.



**FIGURE 8.1.** Butterfly feeding. A monarch butterfly extracting nectar from a flowering butterfly bush.

Animals selectively choose where, on what, and how long to forage, often passing up some food items, such as nectar in some flowers, in favor of others. Animals eat to acquire energy and nutrients for survival and reproduction. How they feed, however, reveals a surprising degree of complexity and a large number of decisions. First, a forager needs to find food. Some animals, like butterflies, feed on food that is hidden (inside a flower). Other animals feed on small, mobile prey or food buried by sand, sediments, or bark, which can be challenging to find. After finding a potential food item, a forager is faced with a decision: Should the item be eaten, or should it be ignored and the search continued? Some prey items, such as large nuts or hard-shelled invertebrates, may require the feeding animal to spend extensive time chewing and crushing the exterior to acquire the food inside. These items may not be worth the time and effort needed to consume them. And when a forager like a bee or a hummingbird finds itself in a patch of flowers, it must decide how long to stay, visiting flowers to extract nectar, before moving on to another patch ([Figure 8.2](#)).

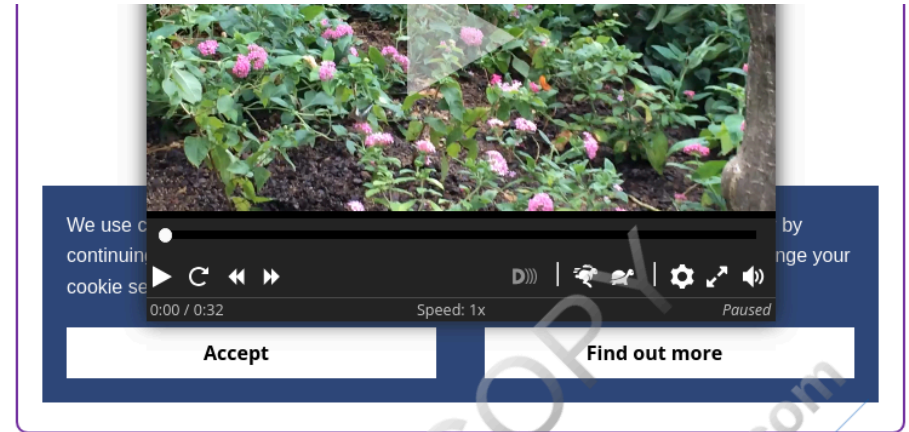


**FIGURE 8.2. Hummingbird and flower.** Flowers differ in the amount of nectar they contain and that nectar's ease of removal.

In this chapter, we first examine how animals use their sensory systems to locate food. Then we focus on animals that use vision to find food and consider how they can more effectively find cryptic prey. Next, we show how mathematical models help us understand how animals select their diet and exploit food patches. Finally, we explore situations in which some individuals usurp the food discoveries of others.

#### Video: Butterflies foraging on flowers

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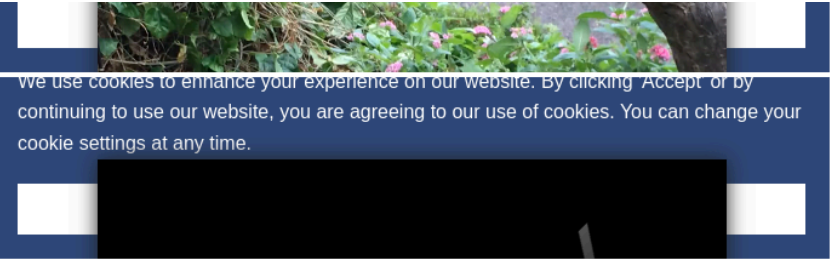
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## 8.1 Animals find food using a variety of sensory modalities

### Learning Objectives

After reading this section, you should be able to

- design a protocol to examine the use of sensory systems in an animal's foraging behavior.

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## behavior and

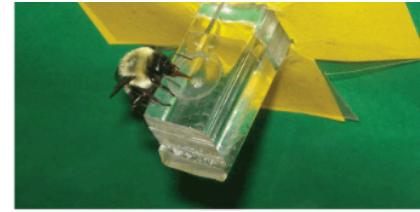
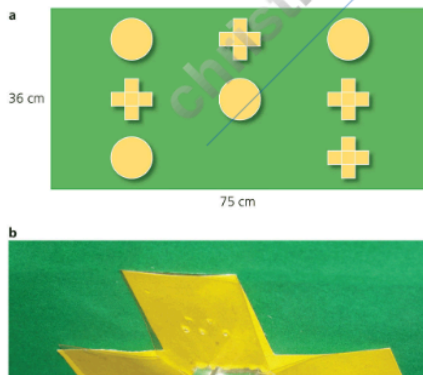
- explain one example showing how the use of multiple sensory systems enhances foraging ability.

Before an animal can eat, it must find food. Recall from [Chapter 5](#) that a variety of sensory systems, or modalities, can be used when animals search for food. Natural selection favors those modalities that most efficiently and accurately provide information about the location of food, but a modality's efficiency can vary with environmental conditions. For instance, visually searching for food in murky water may be difficult. Given the diversity of sensory modalities that an animal possesses, what sensory systems do foragers use to find food? Are some sensory modalities favored over others? Let's examine two examples.

## FEATURED RESEARCH Bees use multiple senses to enhance foraging efficiency

All animals possess multiple sensory systems. This leads to a natural question: Is foraging more efficient when multiple senses are used? Ipek Kulahci, Ana Dornhaus, and Daniel Papaj examined this question in bumblebees (*Bombus impatiens*) ([Kulahci, Dornhaus, & Papaj 2008](#)). Bees feed on nectar and pollen in flowers that can differ in color and shape (visual cues), as well as in odor (olfactory cues). Kulahci and colleagues studied the foraging behavior of individually marked bees to determine how feeding efficiency varies with the number of sensory cues that can be used to find food.

In the laboratory, a box was attached to the colony container. The box had a manual gate that allowed the researchers to release one individual at a time into an experimental arena that contained eight artificial flowers—small circular wells with either 30% sucrose solution (a food reward) or water (no reward). During training, bees were exposed to two yellow flower shapes, circles or crosses, which surrounded the well ([Figure 8.3](#)). Bees were also exposed to two odors: 2  $\mu$ L of either diluted peppermint or clove essential oil that was placed behind the perforated flowers.



**FIGURE 8.3. Bumblebee foraging experiment.** (a) An experimental patch with eight artificial flowers. (b) A bee feeds on a “cross” flower. (Source: [Kulahci, Dornhaus, & Papaj 2008](#))

Individual bees were exposed to one of three training treatments that varied the cues associated with reward flowers. In each treatment, half the flowers (randomly selected) contained sucrose and half contained water. In one treatment, only flower shape (a visual cue) indicated the reward (e.g., crosses indicated reward flowers and circles nonreward flowers, or vice versa). In the second treatment, only odor (an olfactory cue) indicated a reward flower (e.g., peppermint indicated reward flowers and clove nonreward flowers, or vice versa). Finally, in the last treatment, both shape and odor (visual cue plus olfactory cue) indicated reward flowers (e.g., clove plus circle indicated reward flowers and peppermint plus cross indicated nonreward flowers).

During training, bees visited all flowers and eventually learned which ones contained rewards. Training was deemed complete when an individual achieved 80% correct flower choices (reward flowers) over its last ten choices. Once trained, a bee was immediately tested by allowing it to enter the arena, where all the flowers were now nonrewarding. The researchers recorded foraging time spent on each flower and the number of “correct” flower choices the bee made (flowers that the bee had learned contained rewards).

Thirty-one bees were tested. Bees trained on two sensory modalities had significantly higher feeding performance (calculated as correct flower visits divided by total decision time) than bees trained using only a single sensory modality ([Figure 8.4](#)): two-modality bees made more correct choices and spent less time deciding where to feed. These results suggest that the ability to use multiple sensory modes (vision and odor)

These studies illustrate how different species find prey using a variety of sensory modalities. This is only half the story, however. Selection should favor prey that can avoid detection. In the next section, we examine the consequences of prey adaptations that minimize their detection by visual predators.

## 8.2 Visual predators find cryptic prey more effectively by learning a search image

### Learning Objectives

After reading this section, you should be able to

- describe how a search image can enhance foraging efficiency and
- diagram a pattern in data that would indicate that foragers may be using a search image to find cryptic prey.

Many predators, especially birds and mammals like the gray mouse lemur, rely heavily on vision to find prey. This tendency has favored the evolution of behavioral and morphological adaptations in prey species that allow them to blend into their background to avoid being detected by predators. How do predators find it difficult to locate cryptic prey? Perhaps they learn a **search image**, the distinctive visual features of a single prey type (Tinbergen 1960). Evidence for such learning would involve a decrease in the time to find prey with experience. Let's examine one example showing the effectiveness of cryptic coloration for prey and how predators can learn to find such prey more effectively with experience.

### FEATURED RESEARCH Trout and search images

Jörgen Johnsson and Karin Kjallman-Eriksson examined the ability of brown trout (*Salmo trutta*) juveniles (known as parr) to find cryptic or conspicuous prey in a simple laboratory experiment (Johnsson & Kjallman-Eriksson 2008). Brown trout often hunt diurnally and therefore rely more heavily on visual cues for foraging than do nocturnal fish. These animals live in streams and are opportunistic feeders that eat a wide variety of invertebrate prey. Since aquatic invertebrates have different emergence times over the year, trout often have to learn to search for new types of prey as they become available. In addition, trout parr possess tetrachromatic color vision—that is, they have four different types of cone cells, which allow them to see in the red, green, blue, and ultraviolet spectra. This ability to distinguish colors is thought to be an adaptation that allows animals to find cryptic prey.

Johnsson and Kjallman-Eriksson asked two research questions. First, do predators find conspicuous prey more quickly than cryptic prey? Second, does hunting ability improve with experience, as one would expect with the formation of a search image? They predicted that trout would find conspicuous prey in less time than they would

formation of a search image. They predicted that trout would find conspicuous prey in less time than they would find cryptic prey. They also predicted that predators would learn to find a cryptic prey item more effectively as they gained more experience and formed a search image for it (Scientific Process 8.2).

### SCIENTIFIC PROCESS 8.2

Cryptic prey reduces predator efficiency



Research Question: How does cryptic prey coloration affect trout predator foraging efficiency?

#### Hypotheses:

Prey that match their background will be harder for predators to detect, and predator hunting efficiency will increase with experience.

#### Predictions:

Trout will find noncryptic prey faster than they will find cryptic prey. Trout will find cryptic prey faster with experience.

#### Methods:

The researchers:

- Established two test aquaria, identical except for the color of the aquarium bottom: one was brown plastic covered with brown grains, and the other was green plastic covered with green grains.



green grains.

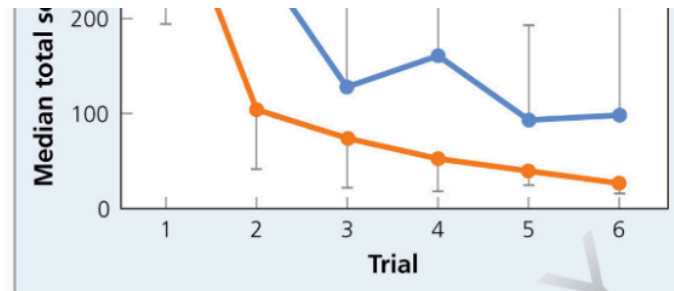
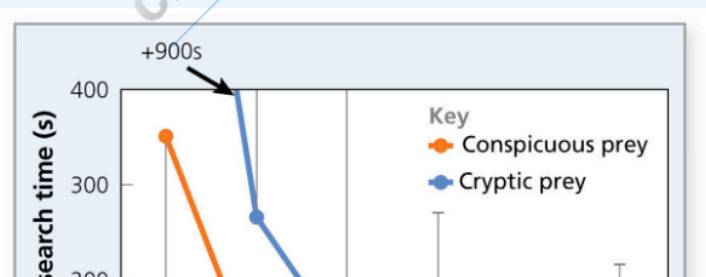
- Placed a single prey (a maggot) in one of six different locations on the aquarium bottom. The maggot was cryptic on the brown background and conspicuous on the green background.
- Recorded the amount of time until the test fish found the food item
- Tested 42 parr, half with cryptic prey and half with conspicuous prey



**FIGURE 1. Background.** The two experimental tanks with differently colored bottoms and scattered prey. (Source: [Johnsson & Kjallman-Eriksson 2008](#))

### Results:

Individuals found noncryptic prey faster than cryptic prey. Search times to find prey decreased with experience.



**FIGURE 2. Search time.** Median search time for conspicuous prey (orange) and cryptic prey (blue). Error bars denote interquartile range, which represents one-quarter of the range of the data. (Source: [Johnsson & Kjallman-Eriksson 2008](#))

### Conclusions:

Background color matching can benefit prey by reducing predator hunting efficiency. Predator search efficiency for cryptic prey can increase over time.

### Evaluate

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Explain how you would determine whether trout hunting ability improves faster with experience when they hunt for cryptic or conspicuous prey.

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The researchers established two test aquaria: one had a bottom covered with brown grains, while the other had a bottom covered with green aquarium grains. Before each trial, a single, small brown maggot (*Calliphoridae* sp.) prey was placed on the aquarium bottom while the test fish was kept behind an opaque partition. The maggot was cryptic on the brown background and conspicuous on the green background. After the maggot was put in place, the partition was lifted and the researchers recorded the amount of time it took the test fish to find the food item.

The trout always found the conspicuous prey faster than the cryptic prey, indicating that foraging efficiency is reduced when predators search for cryptic prey. This means that background color matching can provide significant survival benefits for prey. However, search times decreased over the six trials both when fish searched for cryptic prey and when they searched for conspicuous prey, indicating that trout parr can improve their ability to find prey with only a moderate amount of experience, evidence suggesting they learned a search image of the prey.

Of course, a predator may pay a price for narrowing its focus, as its probability of detecting other prey is thus likely to decrease. You may have experienced this effect if you have ever tried to find an important school paper in your dorm room. You form a mental image of its size, shape, and unique markings. You probably do not pay attention to much else around you as you search. Indeed, a study examining blue jay predators hunting for cryptic moth prey revealed that after jays formed a search image of one moth type, their ability to find other types was reduced (Bond & Kamil, 1999).

### Video: Brown trout and cryptic maggot

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Finding prey is just one aspect of foraging behavior. Animals must also decide, first, which prey types to include (and which not to include) in their diet and, second, how long to spend feeding in one food patch before moving on to another. To address these questions, researchers have developed models based on the assumption that animals attempt to maximize their fitness while feeding. We examine this approach next.

### 8.3 The optimal diet model predicts the food types an animal should include in its diet

Learning Objectives

After reading this section, you should be able to

- summarize the assumptions and predictions of the diet model,
- distinguish a diet generalist from a specialist, and
- determine an optimal diet.

Energy and nutrients are obtained from food, which is limited in most environments. In addition, food is typically heterogeneously distributed in the environment: most places contain little or no food, while other locations, known as food patches, may contain abundant food. For example, a dense aggregation of flowers is a food patch for a bumblebee, and a tree infested with insect larvae is a food patch for a woodpecker.

**Optimal foraging theory (OFT)** assumes that natural selection has favored feeding behaviors that maximize fitness. Many OFT models assume that fitness while feeding is a positive function of an individual's energy intake rate—the energy acquired while feeding divided by total feeding time. OFT models describe the relationship between possible behaviors and the fitness they produce. The behavior that produces the highest fitness is called the **optimal behavior** (Maynard Smith 1978). OFT models provide ultimate (i.e., evolutionary) explanations about the function of behavior. Given a set of possible behaviors and assumed environmental conditions, the models predict the behavior that maximizes fitness and will thus occur in a population (Mitchell & Valone 1990). They are widely used because they produce testable predictions and can be applied to many species and behaviors. Two classic OFT models examine diet and food patch use. Let's start with the diet model, which predicts what food types an animal will consume.

#### The diet model

Animals encounter food types that differ in size, energy content, and handling time—the amount of time it takes to manipulate a food item so that it is ready to eat. Given this diversity, individuals need to decide which food items to eat (i.e., include in their diet) and which to reject. The optimal diet model (Pulliam 1974) is based on three assumptions:

1. Foragers maximize fitness by maximizing energy intake rate.
2. Food items are encountered one at a time and in proportion to their abundance.
3. All food items in the environment can be ranked according to their profitability.

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3. All food items in the environment can be ranked according to their profitability.

The **profitability** of a food item is the energy it contains divided by its handling time. Consider a squirrel feeding on a sunflower seed and a walnut. Sunflower seeds have soft shells and small handling times but also contain relatively little food, or energy, compared to that found in a walnut. The walnut has a hard seed coat and thus a much longer handling time but contains more food, or energy. If the walnut contains 100 joules (J) of energy and takes 25 seconds to consume, its profitability is 4 J/s. If the sunflower seed contains 10 J of energy and has a handling time of one second, its profitability is 10 J/s. In this example, the sunflower seed has higher profitability and so is a higher-ranked food item.

#### A graphical solution

To see how the optimal diet model works, let's first assume that all food types have 10 J of energy (*E*) but differ in handling time (*h*). Table 8.1 shows the handling times for each of five hypothetical food types along with their profitabilities. We see that Type A has the highest profitability, whereas Type E has the lowest. Finally, let's assume that all food types are equally abundant and randomly scattered throughout the environment.

TABLE 8.1 Food item characteristics. Hypothetical food types with their handling times and profitabilities.

Food Type	Energy (J)	Handling Time (S)	Profitability (J/S)
A	10	1	10.0
B	10	3	3.3
C	10	8	1.2
D	10	24	0.4
E	10	29	0.3

What diet maximizes the energy intake rate? Think about this question and write down your answer. You might think that a forager should eat all food items it finds because they all provide it with energy. A forager that eats a wide variety of food types is called a **generalist**, because it has a broad diet and consumes food items in proportion to their availability in the environment. Alternatively, you might think that a forager should maximize its energy intake rate by eating only Type A items because they have the highest profitability. Foragers with restricted diets are called **specialists**, because they consume a small subset of potential food types. Maybe you think that a diet somewhere in between these two extremes should maximize an animal's energy intake rate. At this point, it is not obvious which diet maximizes fitness.

To determine the optimal diet, let's compare the profitabilities of each food type. Type A is the most profitable, so a forager should always include Type A in its diet. What other food types should be added to the diet to maximize energy intake rate (fitness)? You might imagine the five possible diets described in Table 8.2.

TABLE 8.2 Possible forager diets. Five hypothetical diets.

Diet	Eat	Reject	Description
------	-----	--------	-------------

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Diet	Eat	Reject	Description
1	Only Type A	Types B, C, D, and E	Extreme specialist
2	Types A and B	Types C, D, and E	
3	Types A, B, and C	Types D and E	
4	Types A, B, C, and D	Type E	
5	All types	Nothing	Extreme generalist

The first diet is the most specialized and the last the most general. Note that as we move down the list, each diet adds only the next most profitable food item. There are other possible diets, but it makes no sense for a forager to eat a low-ranking food item like Type E while ignoring one of higher profitability like Type A.

We can solve for the optimal diet by computing a forager's average energy intake rate per item in the diet. This is the average energy obtained per item divided by the sum of the average time it takes to find an item and the average time to handle an item in the diet:

$$\text{Average energy intake rate/item} = \frac{(\text{average energy obtained/item})}{[(\text{average search time/item}) + (\text{average handling time/item})]}$$

Because we assumed that all food items contain the same energy, 10 J, the numerator is the same for all diets. We therefore need to know only how the average search time and handling time per item vary with the possible diets. The average search time per food item is the rate at which an individual encounters food in the diet. An individual with a more general diet will have a high encounter rate with food—and thus a lower search time per item—because it eats almost every food item it encounters. An individual with a narrow diet, on the other hand, will have a longer search time per item. Table 8.3 shows how the average search time per item eaten varies for each diet listed in Table 8.2. Note that as more food types are added to the diet, the average search time per item declines.

TABLE 8.3 Mean search time per item for each diet.

Diet	Average Search Time per Item (S)
1	24
2	12
3	8
4	6
5	5

Average handling time per item also varies with diet breadth. From Table 8.1, we can see that if the forager eats only Type A food items, its average handling time per item will be one second. If the diet includes both Type A and Type B items, the average handling time per item will be two seconds (half the items will be Type A, with a handling time of one second, and half will be Type B, with a handling time of three seconds). Table 8.4 shows how the average handling time per item varies for the five possible diets.

TABLE 8.4 Mean handling time per item for each diet.

Diet	Eat	Average Handling Time per Item (S)
1	Only Type A	1
2	Types A and B	$2 = (1 + 3)/2$
3	Types A, B, and C	$4 = (1 + 3 + 8)/3$
4	Types A, B, C, and D	$9 = (1 + 3 + 8 + 24)/4$
5	All types	$13 = (1 + 3 + 8 + 24 + 29)/5$

We can graphically display the average search time per item and average handling time per item for the five possible diets (Figure 8.5). Our graph also shows the combination of search time *plus* handling time per item, which we need to determine the optimal diet. In our example, Diet 3 has the lowest combined search and handling time per item, and so it maximizes the energy intake rate. The model predicts that a forager should always eat Types A, B, and C when encountered and should always reject Types D and E. Why should a forager reject these two types? Because the cost in handling time of including them in the diet is greater than the benefit derived from reduced search time; including these food types in the diet lowers an individual's energy intake rate. The model also predicts that each food type should always be accepted or always be rejected. There is no middle ground. This prediction is called the zero-one rule.

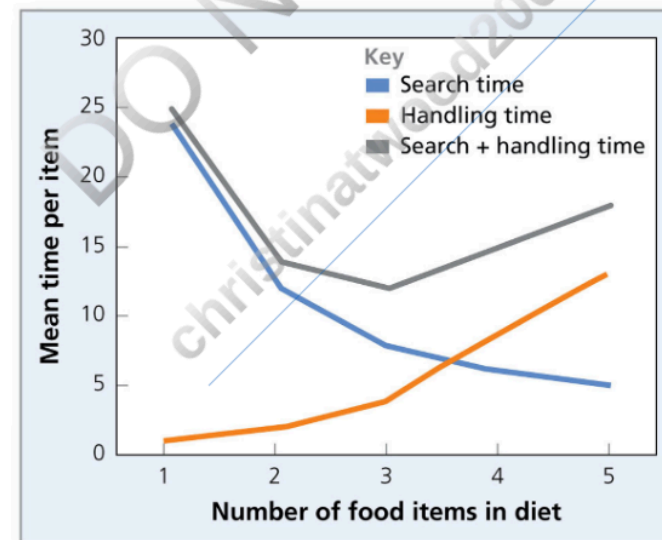


FIGURE 8.5. Diet model solution. A graphical solution for the optimal diet, with lines showing how mean

search time per item (blue) and mean handling time per item (orange) vary with each diet. The optimal diet minimizes mean search time per item plus mean handling time per item (gray).

Now look at the answer you wrote down. Is it the same as the one produced by the model? What logic did you use to generate your prediction? This simple example illustrates the strength of the OFT approach to studying behavior: it makes explicit assumptions and generates predictions that can be tested.

In our example, all food items have the same energy content. We can make the model more general and more realistic by allowing each food item to differ in both energy content and handling time. We can use a mathematical solution to show how this is done (Toolbox 8.1). In general, we find that diet breadth is affected by the abundance of the most profitable prey items, and not by the abundance of the least profitable items.

### TOOLBOX 8.1

#### Mathematical solution to the optimal diet model

For simplicity, assume that there are only two food types in the environment, which we will call Type 1 and Type 2:

1. Type 1 contains an amount of energy ( $E_1$ ) and requires handling time ( $h_1$ ).
2. Type 2 contains an amount of energy ( $E_2$ ) and requires handling time ( $h_2$ ).
3. Type 1 is more profitable because  $E_1/h_1 > E_2/h_2$ .
4. Foragers spend a fixed amount of time searching for food ( $T_s$ ).
5. The food types differ in their abundance in the environment. A forager encounters food Type 1 at a rate of  $\lambda_1$  items per minute searching. Its encounter rate with food Type 2 is  $\lambda_2$  items per minute searching. The inverse of the encounter rate ( $1/\lambda$ ) is the mean search time to find a particular food type.

Since we have only two food types, there are only two possible diets. A forager can specialize on Type 1, the more profitable type, or it can have a general diet and eat both food types. (A third possibility, specializing on Type 2 items, makes no sense, because that is the lower-ranked food type.) Which diet leads to a higher energy intake rate? To answer this question, we compare the energy intake rates of the two possible diets for a forager that searches for time  $T_s$ . We begin with the specialist diet and calculate the total energy acquired and the total handling time. The total energy acquired is simply the number of Type 1 items encountered during search time  $T_s$ —or  $\lambda_1$  multiplied by  $T_s$ —multiplied by the energy,  $E_1$ :

$$\text{Total energy acquired} = (\lambda_1 \times T_s)E_1$$

By the same reasoning, the total handling time of the number of Type 1 items encountered during search time  $T_s$  is the number found ( $\lambda_1 \times T_s$ ) multiplied by their handling time  $h_1$ :

$$\text{Total handling time} = (\lambda \times T_s)h_1$$

and again we know that the total search time is  $T_s$ .

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and again we know that the total search time is  $T_s$ .

The energy intake rate ( $R_1$ ) for the specialist diet is the total energy acquired by feeding on Type 1 items divided by the total search time for those items plus the total time spent handling them:

$$R_1 = \frac{(\lambda_1 \times T_s) \times E_1}{T_s + [(\lambda_1 \times T_s) \times h_1]} \\ = \frac{\lambda_1 \times T_s \times E_1}{T_s \times [1 + \lambda_1 \times h_1]}$$

which simplifies to

$$R_1 = \frac{\lambda_1 \times E_1}{1 + (\lambda_1 \times h_1)}$$

Now we consider the generalist diet. We go through the same steps to calculate the energy intake rate for the generalist diet, but this time we have two terms, one for each food type:

$$\begin{aligned} \text{Total energy acquired} &= [(\lambda_1 \times T_s)E_1] + [(\lambda_2 \times T_s)E_2] \\ \text{Total handling time} &= [(\lambda_1 \times T_s)h_1] + [(\lambda_2 \times T_s)h_2] \end{aligned}$$

where the total search time is again  $T_s$ .

The energy intake rate for this diet ( $R_{1\text{and}2}$ ), is again the total energy acquired divided by the total search time plus the total time spent handling those items:

$$R_{1\text{and}2} = \frac{[(\lambda_1 \times T_s) \times E_1] + [(\lambda_2 \times T_s) \times E_2]}{T_s + [(\lambda_1 \times T_s) \times h_1] + [(\lambda_2 \times T_s) \times h_2]} \\ = \frac{T_s [(\lambda_1 \times E_1) + (\lambda_2 \times E_2)]}{T_s + [(\lambda_1 \times T_s) \times h_1] + [(\lambda_2 \times T_s) \times h_2]}$$

which simplifies to

$$R_{1\text{and}2} = \frac{[(\lambda_1 \times E_1)] + [(\lambda_2 \times E_2)]}{1 + [(\lambda_1 \times h_1) + (\lambda_2 \times h_2)]}$$

A forager should generalize if the energy intake rate from eating both food types is greater than the energy intake rate from specializing on Type 1 only. That means that a forager should be a generalist if  $R_{1\text{and}2} > R_1$ , or

$$\frac{[(\lambda_1 \times E_1) + (\lambda_2 \times E_2)]}{1 + [(\lambda_1 \times h_1) + (\lambda_2 \times h_2)]} > \frac{\lambda_1 \times E_1}{1 + (\lambda_1 \times h_1)}$$

Rearranging produces this inequality:

$$\frac{E_2}{h_2} > \frac{E_1}{\frac{1}{\lambda_1} + h_1}$$

The model predicts that Type 2 should always either be rejected (if the inequality is false) or eaten (if the inequality is true): foragers should always either eat or reject a food type. This prediction is the zero-one rule.

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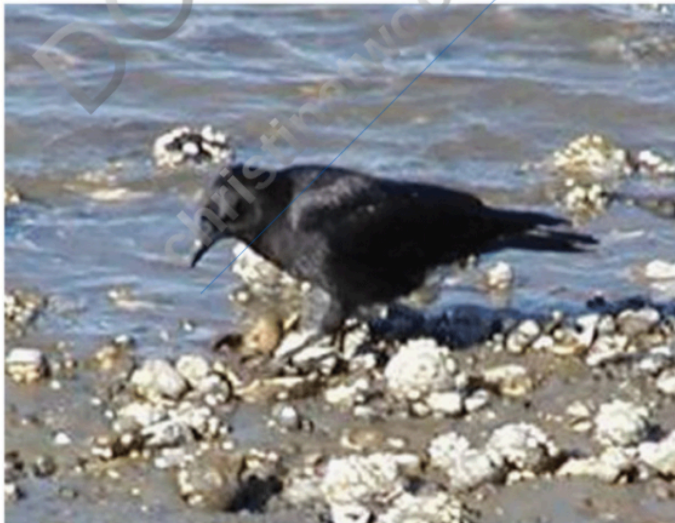
prediction is the zero-one rule.

The model also predicts that the decision to specialize or generalize is not affected by the encounter rate with the lower-ranked food item. The term  $\lambda_2$  does not appear at all in the final inequality. Type 2 could be infinitely abundant, and the forager's diet would still not change. Why not? Look again at the inequality. Just one behavioral difference distinguishes the generalist from the specialist: when an individual finds a Type 2 food item, that item is eaten by the generalist and rejected by the specialist. The forager should eat the item (and be a generalist) if the energy intake rate for that item (the left-hand side of the inequality) is greater than the energy intake rate of rejecting that item instead of searching for a Type 1 item (the right-hand side of the inequality). Since this judgment does not involve finding the Type 2 item, its encounter rate is irrelevant. Thus, we see that diet selection is really about what *not* to eat.

The optimal diet model makes many simplifying assumptions about food types. It also assumes that there are no competitors or predators in the environment and that the forager does not need to search for mates. But remember that the model is a hypothesis that makes a testable prediction; animals will select a diet that maximizes their energy intake rate. Can it predict the diet of real animals? Let's look at one classic field study.

## FEATURED RESEARCH Diet choice in northwestern crows

Howard Richardson and Nicholas Verbeek used the optimal diet model to understand the feeding behavior of northwestern crows (*Corvus caurinus*) on Mitlenatch Island off the coast of British Columbia (Figure 8.6) (Richardson & Verbeek 1986). Crows on this island eat mainly Japanese littleneck clams (*Venerupis japonica*) but often reject clams that they have found. Richardson and Verbeek used the optimal diet model to understand why.



**FIGURE 8.6. Northwestern crow.** These birds feed on a variety of foods, including clams.

Clams on the island range in size from 10 mm to almost 40 mm in length. Crows open clams by dropping them onto rocks repeatedly to break them and then prying open the shells with their bills. To test the model, Richardson and Verbeek needed to measure handling times, the energy content of the clams, and encounter rates (search times for each item). They measured handling times for clams of different sizes in two ways. First, they observed crows feeding on clams of different sizes (ranging from 10 mm to 40 mm) and recorded the time from the first drop until the clam was eaten, which they defined as the handling time. They then collected the empty shell to determine its size so they could see how handling times varied with clam size. Second, in order to increase their sample size and obtain handling time data on all sizes of clams, they dropped over 500 clams of different sizes onto rocks from heights similar to those used by the crows. They measured the number of drops it took (and the corresponding time) until the clam could be pried open with a fingernail.

### Video: Crows dropping oysters to crack shells

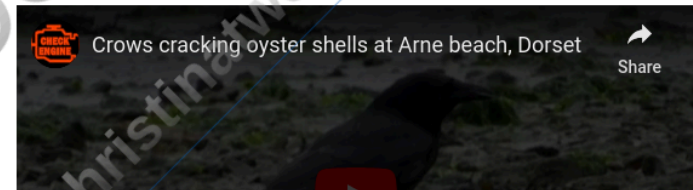
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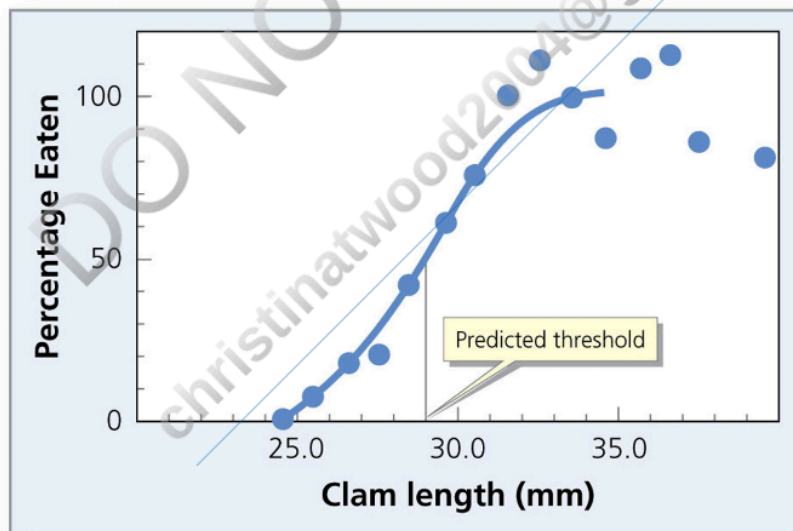
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To measure energy content, the researchers collected and dried the soft tissue from 100 clams of different sizes.



To measure energy content, the researchers collected and dried the soft tissue from 100 clams of different sizes. Previous work allowed them to determine the energy content of a clam based on the amount of dry tissue collected (James & Verbeek 1984). The researchers found that both energy content and handling time increased with clam size. Because both energy content and handling time varied with size, the researchers assumed that clams of different sizes represent different food types. They determined that the largest clam size was the most profitable and that profitability declined as size declined. Finally, they measured the availability of differently sized clams in  $25 \times 25$  cm square plots of land called quadrats. In each of over 200 quadrats, they measured and counted all clams in the top 15 cm of substrate, which was the depth available to crows. These data provided information about the abundance of—and thus encounter rate for—each clam size.

Using this information, the model predicted that crows should eat all clams greater than 29 mm and reject all clams less than 29 mm to maximize their energy intake rate. To test the model, Richardson and Verbeek collected data on the behavior of crows, noting the size of both those clams that were eaten and those that were rejected (clams that were picked up and then ignored). They found that the crows almost always ate clams that were larger than 30 mm and always rejected clams that were less than 26 mm (Figure 8.7). However, the crows did not follow the zero-one rule. Instead, they exhibited a partial preference: they sometimes ate clams of intermediate size. For example, 29 mm clams were eaten about 50% of the time. Although the diet model does not predict partial preferences, overall, the crows' behavior was quite similar to the predicted behavior. Richardson and Verbeek concluded that the observed diet yields an energy intake rate very close to that of the optimal diet.



**FIGURE 8.7. Crow diet choice.** Each data point shows the percentage of clams eaten as a function of clam size. (Source: Richardson & Verbeek 1986)

Many experiments using a variety of animals have produced results that closely match the predictions of the

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many experiments using a variety of animals have produced results that closely match the predictions of the optimal diet model. However, animals often exhibit partial preferences for some food types. Why? The model assumes that foragers have perfect knowledge of the abundance of food types, as well as the energy content and handling times of each type. Of course, real foragers can only estimate these parameters. According to one explanation, the uncertainty results in partial preferences. For instance, the crows probably did not know for sure when they found a 28 mm clam (which the model predicts should be rejected) rather than a 29 mm clam (which should be eaten). Given this uncertainty, it is not surprising that clams of these sizes were sometimes eaten and sometimes rejected. In addition, the diet model assumes that there are no competitors and no predation risk. These factors, too, can lead animals to modify their diet in ways that include exhibiting partial preferences (Bell et al. 1984; Berec & Krivan 2000; Lima, Mitchell, & Roth 2003).

## FEATURED RESEARCH Ant foraging and the effect of nutrients

The optimal diet model assumes that fitness is only a function of energy intake rate. But animals require more than just energy—they also need about two-dozen elements, including carbon, nitrogen, phosphorus, and potassium (Fausto da Silva & Williams 2001). Such dietary needs can affect feeding behavior and diet choice. For example, herbivores often face a situation of sodium limitation because plants contain low sodium concentrations. Thus, many herbivores, ranging from butterflies to large ungulates, are attracted to natural or artificial mineral licks that contain sodium (e.g., Tracy & McNaughton 1995; Boggs & Dau 2004).

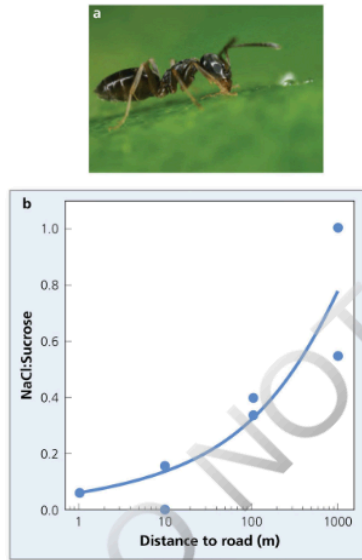
Michael Kaspari, Charlotte Chang, and Johanna Weaver tested the hypothesis that sodium limitation affects the feeding behavior of ants (Kaspari, Chang, & Weaver 2010). They examined the recruitment of ants (attraction to a food source) to two food baits: sucrose (a high-energy food) and sodium chloride (NaCl, or salt). The researchers hypothesized that to maximize their energy acquisition, ants would recruit most heavily to sucrose. However, if sodium is limited and essential, ants should also recruit heavily to it. To examine the relative strength of ant recruitment to the two food sources, the researchers focused on areas that differ in the availability of salt in the environment. Road salt, containing NaCl, is commonly applied to roads in winter. Residual salt can be long lasting and can affect ecosystems near these roads. The researchers predicted that ants living far from salted roads (where sodium is rare) would exhibit a more pronounced preference for NaCl baits than would ants living nearer to salted roads. In other words, environmental availability of sodium should affect the diet selection of ants.

Kaspari and colleagues tested this prediction by establishing two sets of transects in Massachusetts that ran parallel to a road that was salted during winter. Each set contained four transects located 1, 10, 100, and 1,000 m from the road. At 1 m intervals along each transect, the researchers placed a single 2 mL vial on the ground that was half-filled with cotton soaked with either sucrose or NaCl. A total of 90 vials were used in each transect: 45 with sucrose and 45 with NaCl, randomly selected for placement at each point along the transect. One hour later, the researchers collected each vial and recorded any ants inside. At each transect, the researchers also collected soil samples to calculate soil NaCl concentration and thus estimate sodium availability at different distances from the road.

NaCl concentrations were about ten times higher 1 m from the road compared to all other distances, indicating that road salt application does increase sodium availability near roads. About one-third of all ants recorded were *Tapinoma sessile*, a small omnivorous ant that consumes large amounts of vegetation. Near the road, these ants

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strongly recruited to vials containing sucrose: over 90% of the vials visited contained sucrose, and so the NaCl vials were largely ignored. However, as distance from the road increased, ant use of NaCl vials also increased, so that at 1,000 m from the road, there was greater recruitment to the NaCl vials (Figure 8.8). These data demonstrate that sodium limitation affects the feeding behavior of these ants and illustrate how nutrient requirements can affect diet choice. In areas where sodium is limited, animals will often modify their behavior and diet to increase their ingestion of sodium.

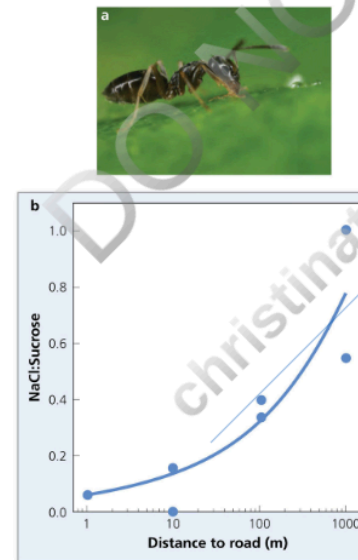


**FIGURE 8.8. Ant NaCl preference.** (a) *Tapinoma sessile*. (b) A greater ratio of NaCl to sucrose vials was used by ants as distance to the salted road increased. (Source: Kaspari, Chang, & Weaver 2010)

Diet choice is one important aspect of a forager's behavior. However, foragers also need to decide how long to exploit one food patch before departing for another. We examine this behavior next.

In other words, environmental availability of sodium should affect the diet selection of ants. Kaspari and colleagues tested this prediction by establishing two sets of transects in Massachusetts that ran parallel to a road that was salted during winter. Each set contained four transects located 1, 10, 100, and 1,000 m from the road. At 1 m intervals along each transect, the researchers placed a single 2 mL vial on the ground that was half-filled with cotton soaked with either sucrose or NaCl. A total of 90 vials were used in each transect: 45 with sucrose and 45 with NaCl, randomly selected for placement at each point along the transect. One hour later, the researchers collected each vial and recorded any ants inside. At each transect, the researchers also collected soil samples to calculate soil NaCl concentration and thus estimate sodium availability at different distances from the road.

NaCl concentrations were about ten times higher 1 m from the road compared to all other distances, indicating that road salt application does increase sodium availability near roads. About one-third of all ants recorded were *Tapinoma sessile*, a small omnivorous ant that consumes large amounts of vegetation. Near the road, these ants strongly recruited to vials containing sucrose: over 90% of the vials visited contained sucrose, and so the NaCl vials were largely ignored. However, as distance from the road increased, ant use of NaCl vials also increased, so that at 1,000 m from the road, there was greater recruitment to the NaCl vials (Figure 8.8). These data demonstrate that sodium limitation affects the feeding behavior of these ants and illustrate how nutrient requirements can affect diet choice. In areas where sodium is limited, animals will often modify their behavior and diet to increase their ingestion of sodium.



**FIGURE 8.8. Ant NaCl preference.** (a) *Tapinoma sessile*. (b) A greater ratio of NaCl to sucrose vials was used by ants as distance to the salted road increased. (Source: Kaspari, Chang, & Weaver 2010)

Diet choice is one important aspect of a forager's behavior. However, foragers also need to decide how long to exploit one food patch before departing for another. We examine this behavior next.

## 8.4 The optimal patch-use model predicts how long a forager should exploit a food patch

### Learning Objectives

After reading this section, you should be able to

- summarize the assumptions and predictions of the optimal patch-use model,
- predict how changes in travel time can affect patch-use time,
- explain how predation risk affects the patch-use model predictions, and
- describe the information used by a forager in Bayesian estimation of food patch quality.

After animals exploit a patch, it can take some time before food is replenished in that patch. For example, after a bee removes nectar from a flower, it can take 24 hours for the nectar to be fully replenished. After a woodpecker removes insects from a tree trunk, it may take days to months before more insect larvae are deposited there. Therefore, when a forager enters a patch with abundant food, it initially harvests food at a high rate, but as the patch becomes depleted, the harvest rate declines: we say that the forager experiences **diminishing returns** as it exploits a food patch. Given diminishing returns, the forager must decide how long to exploit the present (depleting) food patch before abandoning it to search for a richer patch.

To determine the optimal level of patch use, we need to examine the benefit a forager can gain by spending just a bit more time in a patch. This marginal benefit of feeding is the harvest rate at any point in time (or the instantaneous harvest rate). When a forager enters a patch with abundant food, the marginal benefit of feeding is high, because the instantaneous harvest rate is high. Because of diminishing returns, the marginal benefit declines as the patch becomes depleted. When the patch contains little food, the marginal benefit of feeding is very low, because it takes a long time to find the next food item.

### The optimal patch-use model

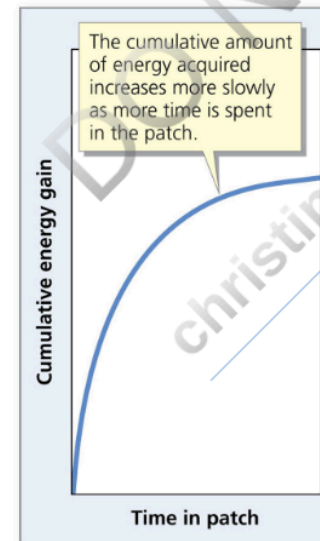
Eric Charnov created an OFT model to predict how long a forager should stay in a food patch to maximize its fitness (Charnov 1976). His optimal patch-use model is based on four assumptions:

1. Foragers attempt to maximize energy intake rate.

2. All patches are identical (contain the same kind and amount of food).
3. Travel time between patches is constant.
4. As a forager depletes a patch, its instantaneous harvest rate declines—that is, it experiences diminishing returns.

Charnov's model, called the **marginal value theorem**, predicts that a forager should stay in a patch until its marginal benefit of feeding declines to equal the average energy intake rate from the environment. This rate is calculated by dividing the total energy acquired from all patches by the total time to travel to and then exploit the patches (travel times plus patch times). In Charnov's original model, the travel time between patches is held constant, and all patches are identical.

How much time should a forager spend in a patch to maximize energy intake rate? To answer this question, we must first determine how much total energy the animal obtains when it stays in a food patch. Initially, there is abundant food in a patch, so the cumulative gain curve begins with a steep slope (Figure 8.9). However, the longer the time spent in a patch, the less food is left (i.e., diminishing returns), and so the curve's slope becomes shallower as more time passes. Next, we need to include the amount of time spent traveling to a patch ( $T_t$ ) in addition to the time spent in the patch ( $T_p$ ). The energy intake rate can now be calculated for any  $T_p$ : it is the energy accumulated, divided by  $T_t$  plus  $T_p$ . We can solve for this relationship graphically, because the energy intake rate for any  $T_p$  is the slope of the line that runs from the start of the travel time to the cumulative gain curve at each  $T_p$ . The patch time that maximizes energy intake rate is the  $T_p$  where this line is tangent to (i.e., just touches) the cumulative energy gain curve (Figure 8.10).



**FIGURE 8.9. Cumulative gain curve.** The graph shows how cumulative energy acquired by the forager



FIGURE 8.10. Cumulative gain curve. The graph shows how cumulative energy acquired by the forager increases with time spent in the patch.

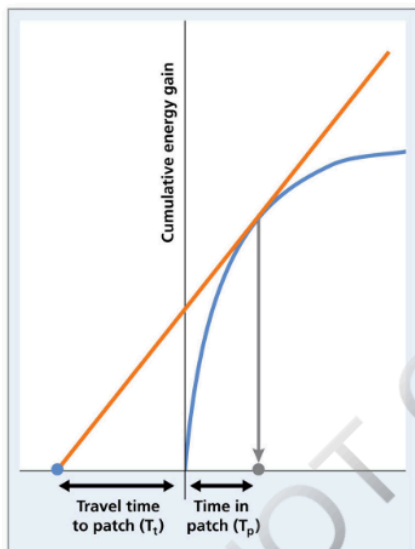


FIGURE 8.10. Marginal value theorem. For a fixed travel time,  $T_t$ , energy intake rate is maximized when the forager spends  $T_p$  time in a patch.

We see that the model predicts the amount of time a forager should spend in a patch for any fixed travel time. This number depends on the travel time: as travel time increases, foragers should spend longer in each patch (Figure 8.11). This prediction can be tested, as we see next.

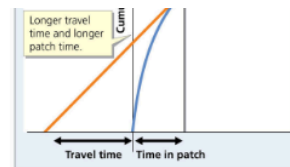
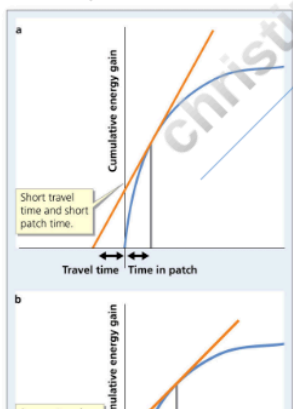


FIGURE 8.11. Travel time and patch time. In (a), travel time between patches is short, and so the optimal patch time is short. In (b), travel time is longer, and so the optimal patch time increases.

## FEATURED RESEARCH Patch use by ruddy ducks

Michael Tome tested the predictions of the marginal value theorem with ruddy ducks (*Oxyura jamaicensis*) (Tome 1988). Ruddy ducks feed on aquatic invertebrates and vegetation on muddy lake bottoms. They repeatedly dive from the water's surface to the lake bottom to find food. A short time later, they emerge to take a breath before diving again for food.

Tome created a large concrete and glass aquarium (5 m long  $\times$  2 m wide  $\times$  2 m deep). The bottom of the aquarium contained 16 wooden trays filled with sand, and the sides had glass windows for observations. Each tray constituted a potential food patch: Tome buried wheat grains in some of the trays during his experiments and trained birds to search the sand for food. The model assumes that ducks would experience diminishing harvest rates while feeding on wheat grains in the artificial food patches. To test this assumption, Tome buried 150 wheat grains in a patch whose location was fixed, which allowed the ducks to learn which patch contained food. He then released a duck to feed from the patch for a fixed amount of time that varied from five to 200 seconds. Afterward, he collected all the wheat grains left in the patch, which told him the amount of food eaten by the duck in that time. He then plotted the number of wheat grains harvested from a patch against time spent in the patch for six ducks (Figure 8.12). He found that the harvest rate did indeed decline as ducks depleted the patch: the cumulative gain (i.e., harvest rate) curve is steep when a bird enters the patch and levels off as the patch becomes depleted. These data match the model's assumption.

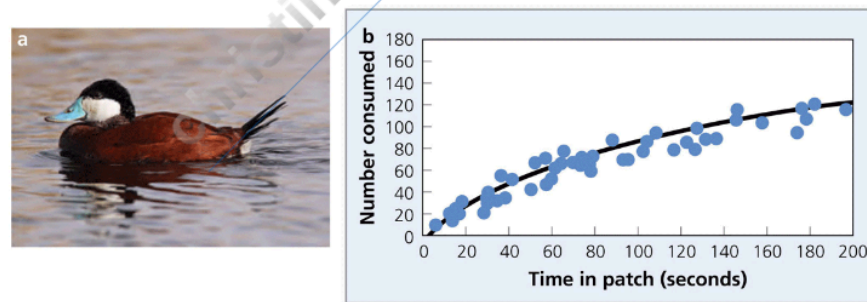
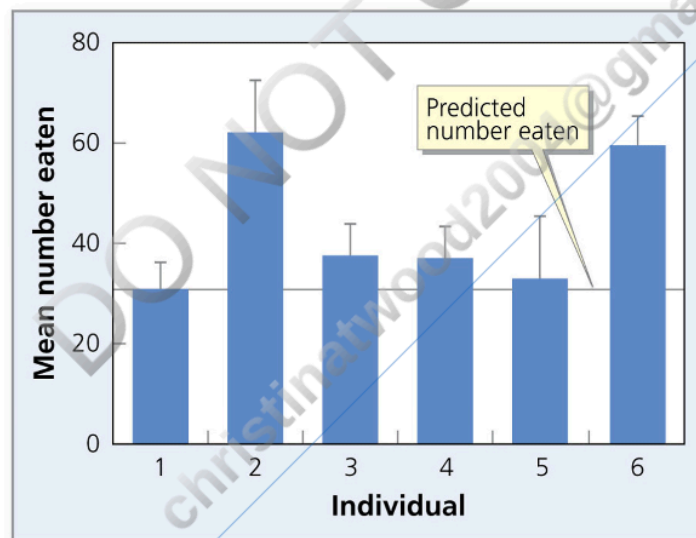


FIGURE 8.12. Ruddy duck cumulative gain curve. (a) Ruddy duck. (b) Number of food items harvested as a function of feeding time in a food patch. (Source: Tome 1988)

Next, Tome established two identical patches on wooden trays placed on the aquarium bottom that each contained 150 buried wheat grains. The locations of each patch were kept constant from trial to trial, and birds were allowed to feed for seven days before the start of trials to learn their location and quality. When a bird first exploited a patch, it dove from the surface. When it abandoned the patch, it returned to the surface to breathe before diving to the second patch. Tome measured the time until a bird abandoned the first patch, as well as the travel time between patches (i.e., the time to travel to the surface to breathe and then dive back down to the second patch).

Tome already knew the relationship between time spent in a patch and the number of wheat grains eaten. From this information, he could calculate the optimal number of food items a bird should eat in a patch to maximize its energy intake rate. To test this prediction, he collected data on the number of food items left in a patch (to determine how many grains were eaten) for the same six birds, conducting ten trials for each.

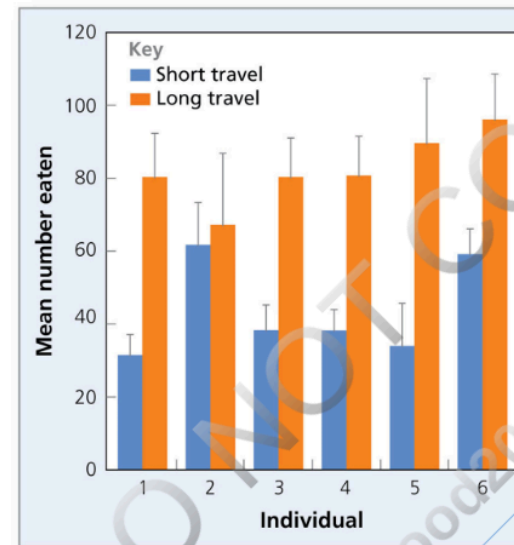
Tome found that the model accurately predicted patch use for the majority of ducks (although two ducks ate more and spent longer in the patches than predicted) (Figure 8.13). He concluded that most of the ducks were maximizing energy intake rate, just as the model assumes.



**FIGURE 8.13. Ruddy duck patch data and prediction.** Mean (+ SE) number of food items eaten by each duck. The line shows the predicted value based on the model. (Source: Tome 1988)

Next, he tested the prediction that a forager should remain longer in a patch as travel time between patches increases. In the first experiment, the travel time between patches was small, because birds learned the location of the two patches and dove directly to them. In a second experiment, Tome increased travel time by randomly changing the location of a single food patch on the aquarium bottom in each trial. This required the ducks to

changing the location of a single food patch on the aquarium bottom in each trial. This required the ducks to search for the patch, and they needed about five search dives (rather than one) before they found it. Tome stopped the trial when a duck abandoned the patch, surfaced, and then dove again to search for other food patches. He again collected the number of food items left in the patch, allowing him to calculate the number eaten. This time, five of the six birds ate significantly more food from the food patch and thus spent significantly more time there, just as the model predicts (Figure 8.14). Tome concluded that the ducks were indeed attempting to maximize their energy intake rate, as assumed by the marginal value theorem.



**FIGURE 8.14. Travel time affects ruddy duck patch-use time.** Mean (+ SE) number of items eaten increased with travel time. (Source: Tome 1988)

The optimal patch-use model is sufficiently general that it can be applied to a variety of species, including humans (Applying the Concepts 8.1). But this model, like the diet model, makes several simplifying assumptions. It assumes that there are no foraging costs other than time spent traveling between and exploiting patches. It also assumes that a forager has perfect information about the environment: it knows that all patches are identical and that the travel time between all patches is the same. Let's see how these assumptions have been modified to better understand the feeding behavior of animals.

## APPLYING THE CONCEPTS 8.1

### Human patch-leaving decisions

Humans are often faced with deciding how long to spend exploiting one resource "patch" before moving to another. For instance, in hunter-gatherer societies, individuals must decide how long

they should search for food in one area before moving to another (Smith & Wishnie 2000). As another example, you may often need to decide how long to hunt for information on one website before changing to another (Pirolli 2005).

John Hutchinson, Andreas Wilke, and Peter Todd evaluated the applicability of the optimal patch-use model to human behavior by presenting 100 subjects with the opportunity to acquire money on a computer fishing game (Hutchinson, Wilke, & Todd 2008). Individuals observed a screen that displayed a cartoon character with a fishing pole (the cursor) at a fishing pond. Fish popped up randomly for two seconds and could be caught by the observer by clicking on them with the mouse. The rate at which fish appeared varied positively with their density in a pond, and harvesting of fish reduced the fish remaining. Individuals could switch to a new pond at any time but could not return to an abandoned one. Moving to a new pond required some travel time during which no fish could be captured. The final payout to the subject depended on the total number of fish captured, so spending too much time at a heavily depleted patch or switching too often (i.e., spending too much time moving and not fishing) would result in poor payoffs. Thus, individuals sought to maximize their gain by determining how long to stay at each pond (patch).

The research team tested individuals on several conditions that varied the distribution of fish in the ponds and the travel time between ponds. Of particular interest were two conditions that had identical resource distributions (a high variance in the number of fish in ponds) but different travel times between each pond (15 seconds or 25 seconds). The model predicts the optimal average time individuals should spend at each patch and that more time should be spent at each patch when travel times are longer. How did the subjects do?

Individuals spent more time than was optimal exploiting the ponds. When travel time was short, they spent an average of 170 seconds at each pond, whereas the optimal average time was 47 seconds. For the longer travel time, individuals spent on average 207 seconds at each pond, while the optimal time was 65 seconds. Note, however, that individuals did increase their patch-use time as travel time increased, as predicted by the model. The researchers suggest that individuals may have spent more time than was optimal exploiting these patches because they needed to learn about the environment, specifically the distribution of fish in the ponds. ■

## Optimal patch model with multiple costs

Joel Brown developed a new patch-use model that includes the energetic costs of foraging, predation risk costs, and missed opportunity costs (Brown 1988). **Energetic costs of foraging** include the energy used to exploit a patch and the metabolic costs

What is that probability? You can determine this number by observing the cards that have already been played. This is the sample information, and it allows you to estimate the frequency distribution of the cards remaining in the deck. If many cards of low value (say, less than eight) have already been played, the probability of drawing a high card is higher, and you are more likely to bust. If many cards of high value (say, greater than seven) have already been played, the probability that the next card will make you bust is much lower. If you did not know the cards in a standard playing deck, the game would be much more difficult. It is the ability to track sample information that so often separates winners from losers at the blackjack table.

Combining prior knowledge with sample information is a powerful way to estimate unknown parameters. How does this skill relate to animal behavior? Modifications of the optimal patch-use model assume that animals estimate food patches much as blackjack players estimate the likelihood that one more card will result in going bust. This process of combining sample information and prior knowledge is called Bayesian estimation because it is done mathematically using Bayes's theorem. Let's examine one recent test of this idea.

## FEATURED RESEARCH Bayesian foraging bumblebees

To answer the question of whether bumblebees estimate food patches in a Bayesian manner, Jay Biernaskie, Steven Walker, and Robert Gegear created an enclosure that allowed a single bee to search artificial flowers for sugar water (Biernaskie, Walker, & Gegear 2009). They made artificial flowers using microcentrifuge tubes that contained either sugar water (a food reward) or plain water (no food). They then created a foraging arena that contained ten food patches comprising 12 artificial flowers each (Figure 8.17). Using this design, they trained individual bees to learn different distributions of patch types. This information became the bee's prior knowledge. One set of bees learned that all patches were the same: five flowers contained rewards and seven flowers did not; hence, the mean rewards per patch were five.

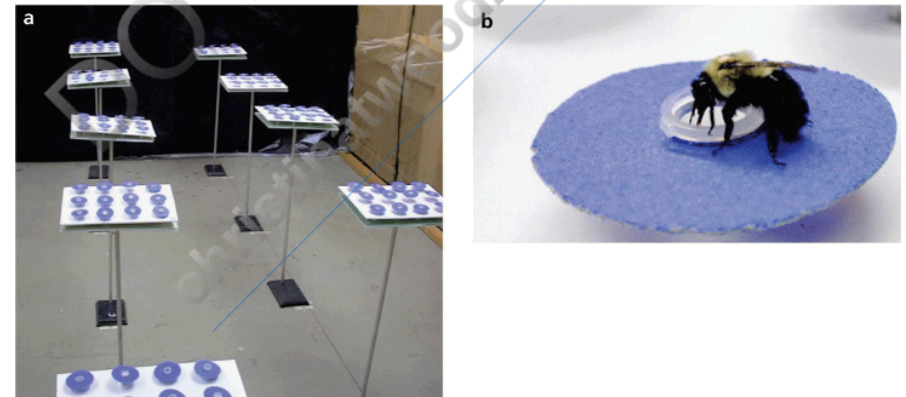


FIGURE 8.17. Foraging arena. (a) Food patches with 12 artificial flowers each. (b) Bee exploiting a flower.

The location of the rewards was randomly assigned within each patch, so the bees could not memorize the exact location of rewards within patches. Such a condition is called a uniform environment because there is no variation in the number of rewards across patches. More formally, patch variance in this distribution of patch types was



in the number of rewards across patches. More formally, patch variance in this distribution of patch types was zero. The researchers predicted that the patch quality estimate of bees trained in this uniform environment should decline each time the bees found a food reward, because this would indicate the presence of one less food reward in that patch. Finding rewards represents the bees' sampling information. This leads to our first prediction:

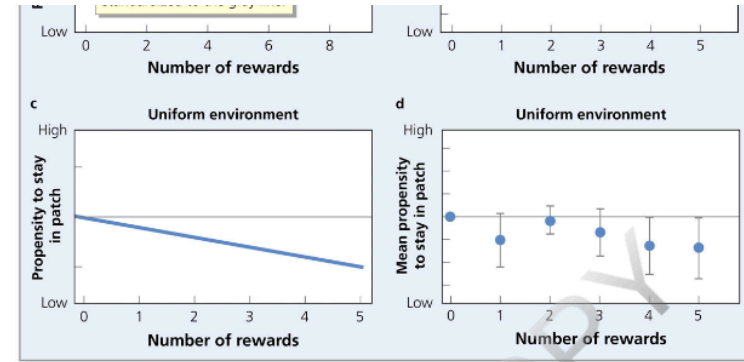
**Prediction 1:** Bees trained in the uniform environment should have a lower probability of staying in a patch after each reward is found, and they should always immediately leave after finding the fifth reward.

A second set of bees was trained in a high-variance environment. Here, half the patches contained nine rewards, and half the patches contained one reward. The mean patch in this environment contained five rewards (as in the uniform environment), but the variation in rewards among patches was much higher. For bees trained in the high-variance environment, there was a different relationship between the number of rewards found and the expected number of rewards left in the patch. A bee using prior knowledge of the high-variance environment could now learn about the quality of a patch from sampling information. After finding one reward, it would know that there was a 50% chance the patch contained eight more rewards, and so the estimated patch quality would be relatively high. Once a bee found a second reward, it would know with 100% certainty that the patch contained seven more rewards, and so the estimate of the patch would be very high. After that, each reward found would mean that one fewer was left, and so the estimate of the patch quality would decline. This generates our second prediction:

**Prediction 2:** If bees use prior knowledge, individuals trained in the high-variance environment should have a high probability of staying in the patch after finding the second reward. The probability should decline thereafter.

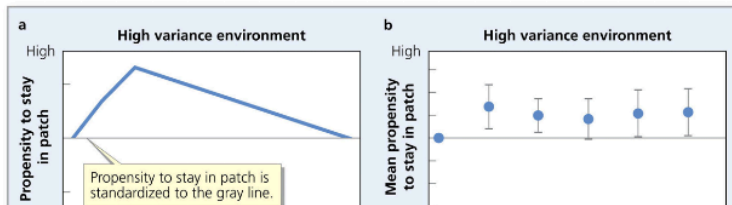
The research team tested these predictions using 20 bees, half of which were trained in each environment, that fed on patches in a test environment. For each bee, the researchers recorded the number of flowers visited and how often the bee left a patch after finding a reward. This procedure was repeated for ten test patches for each bee.

As predicted, bees trained in the uniform environment had a lower probability of staying in the patch for each reward found. Bees in the high-variance environment, on the other hand, showed a much higher probability of remaining in the patch after finding the second reward compared to bees trained in the uniform environment. The likelihood of patch departure, however, did not decline for each reward found thereafter (Figure 8.18). In general, these results are consistent with the idea that bees can learn different prior distributions. The data also suggest that bees combine information from prior distributions with sample information. It is important to note that these animals are not calculating probabilities. Rather, they display adaptive learning regarding the distribution of resources in their environment. Such estimation allows them to exploit food patches more efficiently. A wide variety of animals, ranging from insects to mammals, do the same (Valone 2006).



**FIGURE 8.18. Predicted and observed patch-leaving behavior.** (a and c) Predicted propensity to remain in a patch as a function of the number of rewards found in each environment. (b and d) Observed ( $\pm$  error bar) propensity to stay in a patch as a function of the number of rewards found in each environment. (Source: [Biermaskie, Walker, & Gegeer 2009](#))

The original optimal foraging models are based on many simplifying assumptions. Recent work has incorporated more realistic assumptions about the environment (e.g., patches have different initial amounts of food) and the forager (e.g., multiple foraging costs and incomplete knowledge about food patch quality). Although these models may still seem somewhat simplistic, they have been remarkably successful at predicting complex foraging behaviors in a wide variety of animals.



## 8.5 Some animals obtain food from the discoveries of others

### Learning Objectives

After reading this section, you should be able to

- differentiate scroungers from producers in a group of animals and
- explain the predicted equilibrium frequency of producers and scroungers in a group.

Throughout this chapter, we have examined the foraging behavior of individuals, independent of the behavior of others. But some foragers are kleptoparasites: they obtain food from other individuals. Heterospecific kleptoparasites usurp food from a different species (Iyengar 2008). Such behavior not only reduces search costs but can also increase diet breadth. For example, Stéphane Morissette and John Himmelman quantified the success of kleptoparasites that steal food from the sea star (*Leptasterias polaris*) (Morissette & Himmelman 2000). This echinoderm extracts large buried clams from the sediment to feed on them, a process that can last for several days (Figure 8.19). A variety of opportunistic carnivores that cannot extract and feed on large buried clams rely on kleptoparasitism to obtain such food. These kleptoparasites include whelks, crabs, and another sea star, *Asterias vulgaris*.



FIGURE 8.19. Sea star eating clam. *Leptasterias polaris* opening a clam to eat.

To document interactions among these species, Morissette and Himmelman used underwater cameras at a study site in the Gulf of Saint Lawrence to film 20 *L. polaris* individuals feeding on a large clam provided by the researchers. The researchers estimated the mass of the clam before and after it was eaten by *L. polaris*, both when kleptoparasites were excluded by a cage and when they were present. This allowed the research team to determine how much food mass, on average, was lost to kleptoparasites.

After the initiation of feeding, kleptoparasites arrived within a few hours and frequently contacted the feeding sea star when not excluded by a cage. Such interactions sometimes lasted several hours, and all kleptoparasites successfully obtained food from the clam prey: the sea star lost 6%–20% of clam prey mass to the heterospecific kleptoparasites.

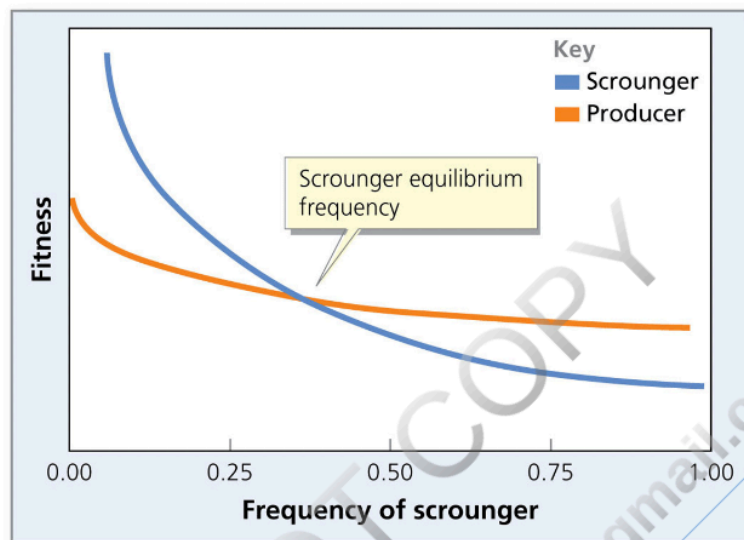
In this marine system, a variety of species gain access to a unique resource via kleptoparasitism of food captured by the heterospecific *L. polaris*. Perhaps even more often, however, individuals obtain food from the food discoveries of conspecifics, as we see next.

### FEATURED RESEARCH Spice finch producer-scrounger game

Some individuals within stable social groups often usurp food from conspecifics. In such cases, we classify individuals that search for and find food as **producers**, while those that usurp food from producers are called **scroungers**.

The existence of conspecific producers and scroungers within a foraging group is particularly interesting because successful scrounging requires at least one producer: no one obtains food if all group members are scroungers. Furthermore, as the proportion of scroungers increases in a group, fewer scrounging opportunities will exist. One might correctly conclude that the foraging success (fitness) of scroungers should be high when they are rare relative to producers in a group but should decline as the frequency of scroungers in the group increases. Given this relationship, what frequency of scroungers might we expect in a foraging group?

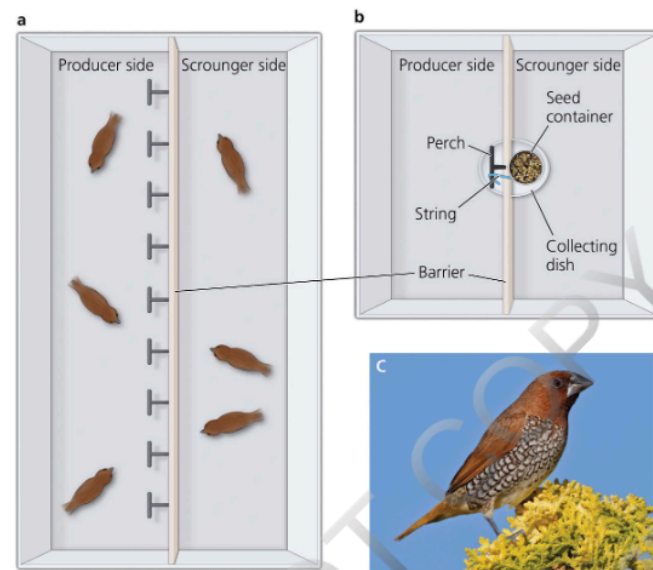
The producer-scrounger game theory model was developed to answer this question (Barnard & Sibley 1981; Vickery et al. 1991). This model assumes that searching for (and finding) food is incompatible with searching for scrounging opportunities. This might often be true when finding food requires searching the ground (head down), whereas searching for successful scrounging opportunities requires scanning the environment to observe producers (head up). The model also assumes that the feeding rate (fitness) of scroungers decreases as the frequency of scroungers in the group increases, so that the fitness of scroungers is higher than that of producers when scroungers are rare but lower than that of producers when scroungers are common. The model predicts that there is an equilibrium frequency of scroungers and producers at which their fitness is equal (Figure 8.20): both behavioral strategies can persist in a population at this stable equilibrium.



**FIGURE 8.20. Producer-scrounger model.** Hypothetical payoffs (fitness) of the scrounger (blue line) and producer (orange line) strategies as a function of scrounger frequency in a group. The intersection denotes the predicted frequency of scroungers in groups. (Source: Mottley & Giraldeau 2000)

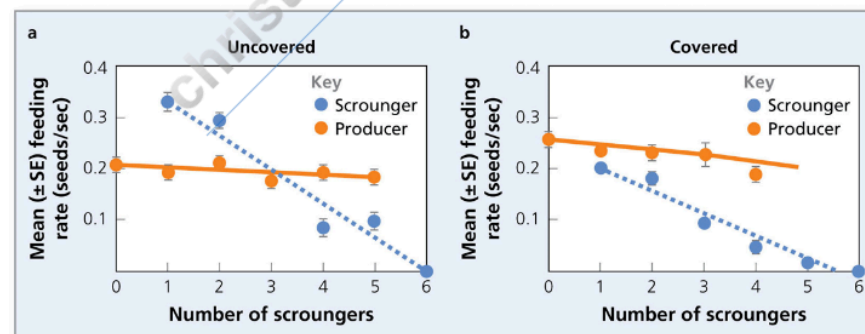
Kiemon Mottley and Luc-Alain Giraldeau tested the producer-scrounger model using captive flocks of spice finches (*Lonchura punctulata*), a granivorous bird native to Southeast Asia (Mottley & Giraldeau 2000). These birds exhibit little aggression, and in captivity, individuals can behave as both producers and scroungers (Giraldeau, Sops, & Beauchamp 1994). Mottley and Giraldeau trained birds to feed from two sides of a set of artificial patches that contained seeds. On one side of the patches, individuals were producers, while on the other side, they were scroungers. Birds were trained to pull a string on the producer side of the patch, which caused seeds to fall into a collecting dish. Seeds in the dish were accessible to the producer that pulled the string and to all scroungers on the other side.

The researchers then formed multiple flocks of six birds. Each flock had differing numbers of producers and scroungers because each individual was restricted to just one side of the food patch (producers on one side, scroungers on the other) (Figure 8.21). This allowed the research team to create six treatments that manipulated the proportion of producers and scroungers in a flock, ranging from one producer and five scroungers to six producers and zero scroungers. This procedure was replicated for three different flocks. One final manipulation affected the benefit of scrounging. When the food patches were uncovered, scroungers had ready access to seeds that fell into the collecting dish. However, when the patches were covered, scrounger access was more limited, slowing their ability to obtain seeds and so reducing the benefit of scrounging. In each trial, a focal individual was observed to determine its feeding rate.



**FIGURE 8.21. Producer-scrounger experimental setup.** (a) Producers and scroungers were restricted to separate sides of the arena. (b) When producers pulled the string, seeds fell into a container from which both producers and scroungers could feed. (c) Spice finch. (Source: Mottley & Giraldeau 2000)

The feeding rate for scroungers was indeed lower when patches were covered for all flock types. As expected, for both uncovered and covered patches, the feeding rate of scroungers declined as the proportion of scroungers increased (Figure 8.22). In contrast, the feeding rate of producers was largely unaffected by the proportion of scroungers for both types of patches. For uncovered patches, producers and scroungers had equal fitness when they were equally common; for covered patches, scroungers and producers had equal fitness when a flock had one scrounger and five producers.

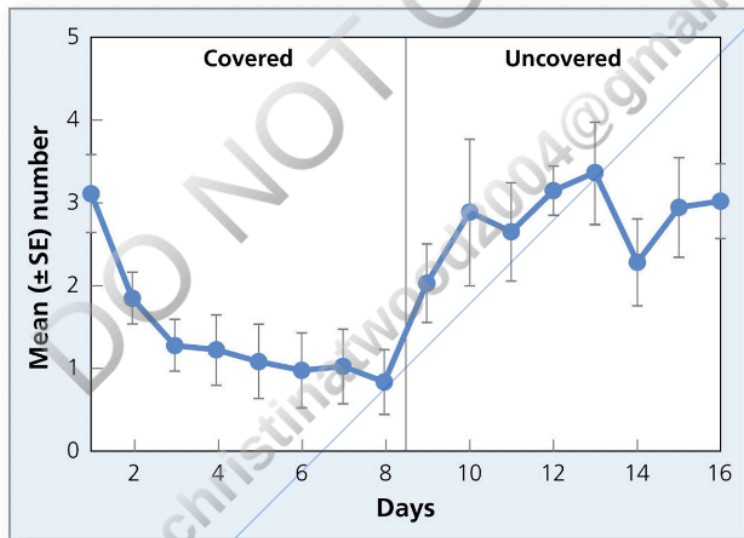




**FIGURE 8.22. Producer and scrounger feeding rates.** (a) For uncovered patches, producer (orange circles and line) and scrounger (blue circles and line) feeding rates were equal when flocks contained three scroungers. (b) For covered patches, producers (orange) and scroungers (blue) had equal feeding rates only when there was a single scrounger. (Source: [Mottley & Giraldeau 2000](#))

Next, Mottley and Giraldeau examined how birds would behave when all were free to use either side of the patch. Would flocks of birds conform to the predicted proportions of producers and scroungers? In the second experiment, the patch was covered for Days 1–8 and uncovered for Days 9–16. The researchers again measured the behavior of focal individuals in three different flocks, noting their foraging strategy (producer or scrounger) and their feeding rate.

Individual birds tended to adopt one or the other foraging strategy, although there was some switching of patch sides at the start of a trial. In just a few days, the flocks adjusted their scrounger frequency to the predicted values: for covered patches, flocks contained about one scrounger, while for uncovered patches, there were about three scroungers per flock ([Figure 8.23](#)).



**FIGURE 8.23. Number of scroungers.** For covered patches (Days 1–8), flocks tended to have a single scrounger. For uncovered patches (Days 9–16), flocks contained about three scroungers. (Source: [Mottley & Giraldeau 2000](#))

These data are consistent with the predictions of the producer-scrounger model, which assumes that individuals attempt to maximize feeding rate. This suggests that foraging spice finches are capable of fine-scale adjustments in their behavior based on current environmental condition (the benefit of scrounging) and the behavior of others.

Within stable groups of conspecifics, some individuals find food while others usurp those discoveries, but within

## CHAPTER SUMMARY AND BEYOND

Animals find food using a variety of sensory modalities. Many foragers locate food visually and have trouble finding cryptic, as opposed to conspicuous, prey. Animals can increase their hunting success on cryptic prey by forming a search image that allows them to focus on a single prey type. Research has examined interactions among prey camouflage, predator search images, and the evolution of prey polymorphisms ([Bond 2007](#)). In addition, olfactory search images are being used to train dogs to identify explosive materials ([Gazit, Goldblatt, & Terkel 2005](#)).

Optimal foraging theory assumes that natural selection has favored behaviors that maximize fitness largely by maximizing energy intake rate, and it has become a powerful approach to studying the behavior of animals ([Rosenzweig 2001](#)). The optimal diet model is used to understand the diet breadth of foragers. This model predicts that animals should adopt a zero-one rule for each food type and that diet breadth should be affected by the abundance of the most profitable food items and not by the abundance of the least profitable items. [Sih and Christensen \(2001\)](#) provide a comprehensive review of studies that have tested this model. Their review finds good support for the model, especially for foragers that consume immobile prey items.

The optimal patch-use model predicts how long a forager should remain in a patch. It predicts that foragers should spend longer in patches as travel time increases, and empirical tests show that it does often successfully predict behavior. Modification of the patch-use model includes the addition of energetic, predation risk, and missed opportunity costs of foraging. [Brown and Kotler \(2004\)](#) show how incorporation of these costs provides even greater understanding of feeding behavior.

While the optimal patch-use model assumes that animals have perfect knowledge of the food patches they encounter, most animals must estimate the quality of a food patch. Many appear to do so by combining prior knowledge about the distribution of patch types in the environment with current sampling information from a patch in a manner similar to Bayesian updating. [Valone's \(2006\)](#) review shows that many animals, including mammals, birds, fish, and insects, are capable of making such estimates.

Many animals usurp food that has been discovered by others. Such kleptoparasitism can enhance diet breadth and reduce search time for food. Within a social group of conspecifics, there often will exist variation in feeding behavior: producers search for food, while scroungers obtain food discovered by producers. The producer-scrounger model explains this diversity and predicts the equilibrium frequency of each strategy in a group. Recent work has investigated how often these strategies are fixed or flexible ([Morand-Ferron, Varennes, & Giraldeau 2011](#); [Harten et al. 2018](#)) and how individual condition affects the adoption of these strategies ([David & Giraldeau 2011](#)).

## Chapter Summary and Beyond

Animals find food using a variety of sensory modalities. Many foragers locate food visually and have trouble finding cryptic, as opposed to conspicuous, prey. Animals can increase their hunting success on cryptic prey by forming a search image that allows them to focus on a single prey type. Research has examined interactions among prey camouflage, predator search images, and the evolution of prey polymorphisms ([Bond 2007](#)). In addition, olfactory search images are being used to train dogs to identify explosive materials ([Gazit, Goldblatt, & Terkel 2005](#)).

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## CHAPTER REVIEW

### 8.1 Animals find food using a variety of sensory modalities

- Bees forage more efficiently when they can use multiple sensory systems to find food.
- Grey mouse lemur ability to find food increases with the number of sensory systems employed.

### 8.2 Visual predators find cryptic prey more effectively by learning a search image

- A search image allows foragers to more effectively find cryptic food.
- Trout find prey faster with experience, as they form a search image.

### 8.3 The optimal diet model predicts the food types an animal should include in its diet

- The diet model predicts which food items should be eaten and which ignored to maximize energy intake rate.
- Northwestern crows maximize their energy intake rate by consuming clams over a specific size.
- Ant foraging is influenced by energy intake and the need for sodium.

### 8.4 The optimal patch-use model predicts how long a forager should exploit a food patch

- Individuals should exploit a patch until the marginal benefit of feeding equals the average energy intake rate of the environment.
- Ruddy ducks exploit food patches in a way that maximizes energy intake rate.
- Foragers should balance the benefits of feeding with all of the energetic, predation risk, and missed opportunity costs.
- Fruit bats equalize giving-up densities in different food patches as they balance foraging benefits and costs.
- Kangaroo rats foraging behavior is affected by perceived predation risk costs.
- Bees estimate the quality of a food patch based on past experience.

### 8.5 Some animals obtain food from the discoveries of others

- Kleptoparasites obtain food from other individuals.
- Producers find food patches; scroungers exploit food patches found by producers.
- Spice finch producers and scroungers can obtain equal fitness by adjusting the frequency of each in a group.

• Ruddy ducks exploit food patches in a way that maximizes energy intake rate.

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## CHAPTER 7

# Learning, Neuroethology, and Cognition

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 7.1 [Learning allows animals to adapt to their environment](#)
- 7.2 [Learning is associated with neurological changes](#)
- 7.3 [Animals learn associations between stimuli and responses](#)
- 7.4 [Social interactions facilitate learning](#)
- 7.5 [Social learning can lead to the development of animal traditions and culture](#)
- 7.6 [Animals vary in their cognitive abilities](#)

### Features

- |                               |   |
|-------------------------------|---|
| <b>Scientific Process</b>     | 7.1 <a href="#">Brain structure and food hoarding</a>             |
|                               | 7.2 <a href="#">Fish learn predators</a>                          |
| <b>Applying the Concepts</b>  | 7.1 <a href="#">Operation Migration and imprinting</a>            |
|                               | 7.2 <a href="#">Dog training</a>                                  |
|                               | 7.3 <a href="#">Human social learning about dangerous animals</a> |
| <b>Quantitative Reasoning</b> | 7.1 <a href="#">Aggressiveness and learning ability</a>           |

Many years ago, during an ornithology class field trip to the Chiricahua Mountains of southeastern Arizona, we heard a loud whistle nearby. Almost instantly, we began to hear vocalizations of a flock of Mexican jays (*Aphelocoma wollweberi*) that appeared to be moving toward the location of the whistle (Figure 7.1). We followed the jays to find a researcher who was busy collecting data on aggressive behavior.



**FIGURE 7.1.** Mexican jay. These birds learned to associate a whistle with the presence of food.

This flock was being studied by Jerram Brown and his students. They had uniquely color-banded individuals and were investigating the behavior and ecology of these social birds. In Brown's early work, researchers placed small piles of food in the center of a flock's territory to attract many individuals, who then competed for access to the food. One year the researchers blew a police whistle a few times just before putting out the food, and soon the jays learned to associate this novel sound with the presence of food at a specific location. Over time, the researchers noticed that yearlings learned the association from older birds, with unmarked young birds quickly responding to the sound even though no whistle had been blown in the area for almost a year (Brown 1997b).

In this chapter we examine the broad array of ways that animals learn, ranging from simple habituation to complex problem solving. We also examine the physical changes in the brain that are associated with learning. We then discuss individual and social learning and see how the latter can lead to the development of animal traditions and even culture. We end by discussing animal cognition.

### Video: Mexican jays calling

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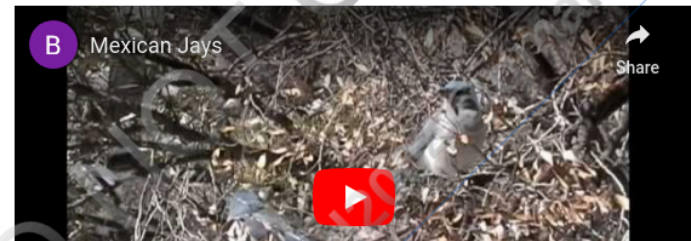
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### 7.1 Learning allows animals to adapt to their environment

#### Learning Objectives

After reading this section, you should be able to



- identify learning,
- predict when selection will favor the evolution of learning, and
- explain why the example of habituation in fiddler crabs is an example of adaptive learning.

**Learning** is a relatively permanent change in behavior as a result of experience. It is a process by which animals modify their behavior, or adapt to their environment, in ways that allow them to experience increased fitness. For example, the ability to capture prey successfully is a foraging skill that can affect fitness and improve with experience, as we see next.

## FEATURED RESEARCH Improved foraging efficiency in salamanders

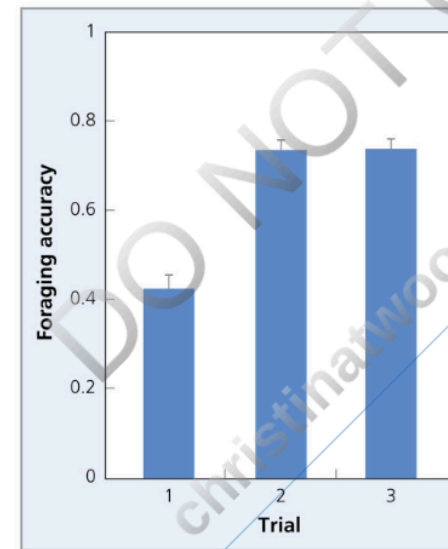
Red-backed salamanders (*Plethodon cinereus*) are common in the eastern deciduous forests of North America (Figure 7.2). They feed under rocks and logs on a wide variety of invertebrate prey. Salamander neonates can recognize, attack, and capture prey within one week of hatching, without prior experience. Does their foraging efficiency improve with experience? Megan Gibbons, Arianne Ferguson, and Danielle Lee conducted an experiment to investigate the hypothesis that learning would improve salamanders' skill as predators (Gibbons et al. 2005).



**FIGURE 7.2.** Red-backed salamander. This salamander feeds on small invertebrates.

Gibbons and her colleagues examined the predatory hunting skill of lab-reared two-week-old individuals that had no prior opportunity to forage. To standardize hunger levels, three feeding trials were separated by about 14 days, the digestion period for these neonates. To characterize feeding efficiency, the researchers presented four termites (*Reticulitermes flavipes*) to an individual and recorded capture attempts (a jaw snap at one termite), successful captures, and the number of prey that escaped after capture in each ten-minute trial. From these data, they calculated the salamanders' foraging accuracy (measured as the number of prey eaten, divided by the number of attacks, captures, and escapes).

They found that neonates captured few prey during the first trial. The proportion captured improved dramatically, however, in Trials 2 and 3 (Figure 7.3). These data suggest that individuals rapidly learned to forage in a more efficient manner as they gained experience. In this example, only one learning experience was required for a large gain in foraging efficiency. Such improved performance can enhance survivorship in the wild.



**FIGURE 7.3.** Salamander foraging accuracy. Mean (+ SE) foraging accuracy of prey capture increased after one trial. (Source: Gibbons, Ferguson, & Lee 2005)

## Evolution of learning

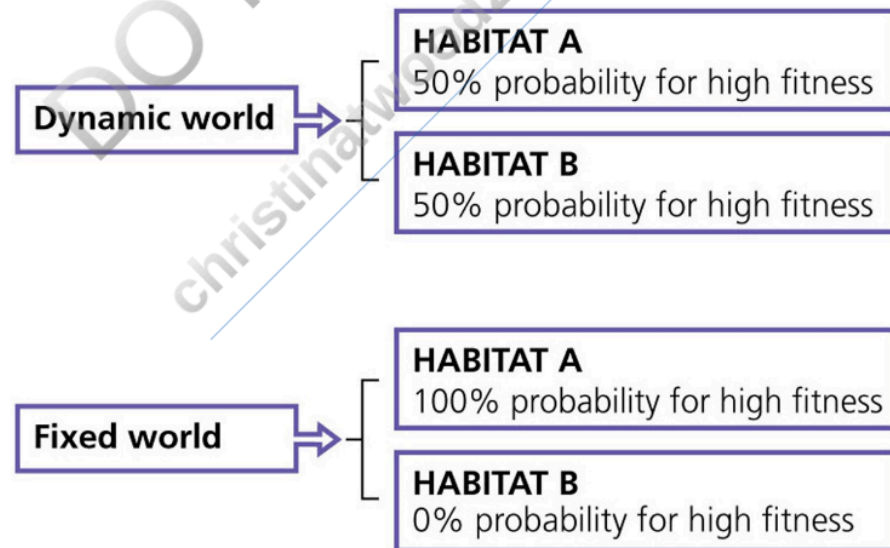
In the previous example, individuals learned to hunt more effectively, a skill that should improve their fitness.

This finding raises the question, "Is learning always adaptive?" A long-standing answer was that evolution should

This finding raises the question, “Is learning always adaptive?” A long-standing answer was that evolution should always favor improved learning ability in dynamic environments. However, the answer may be more complex.

Theory indicates that two factors affect the evolution of learning: environmental stability and the usefulness of past experience (e.g., [Mery & Kawecki 2002](#); [Dunlap & Stephens 2009](#)). Consider two possible types of worlds: one is fixed and experiences no change (e.g., no new predators or parasites ever appear), while the other is dynamic and changes unpredictably (e.g., new predators and parasites may appear in the middle of the breeding season). Now imagine two habitats (A and B) that differ in quality for reproduction: breeding in one leads to high fitness, while breeding in the other leads to reproductive failure. In the fixed world, the high-fitness habitat (A) will always be the best place to reproduce. In the dynamic world, both habitats have the possibility of leading to high fitness due to the unpredictable nature of predators and parasites. Sometimes A will be best and at other times B will be best.

Now let’s assume that in this changing dynamic world, each habitat has a 50% chance each breeding season of being high quality or causing reproductive failure ([Figure 7.4](#)). In which world should learning evolve? Neither. This answer may not be intuitive, so let’s examine why. In the fixed world, individuals that breed in the high-fitness habitat will quickly outcompete those that reproduce in the other habitat. If habitat choice is influenced by genes, the world will soon be full of individuals that selected only the high-fitness habitat, and there would be no need to learn about the other habitat or the differences between them. On the other hand, in the dynamic world, there is nothing to learn, because learning is useful only if individuals can benefit from their experience. In other words, there must be a predictable relationship between experience and the best option available at a given moment. In the dynamic world, the habitats change unpredictably, and so both habitats always have a 50% chance of being the best option, no matter what happened in the past. Again, there is no benefit to learning because information about the environment has no value.



**FIGURE 7.4. Dynamic and fixed worlds.** In a dynamic world, reproduction in each habitat can lead to high fitness, but in a fixed world, only one habitat leads to high fitness.

Learning theory thus demonstrates that two factors affect the evolution of learning: the regularity of the environment and the reliability of past experience. These factors are independent of each other but are not mutually exclusive. As environmental regularity increases, learning will become less favored, because in a completely regular world, evolution will fix behavior. As the reliability of experience increases, learning will be strongly favored, because individuals that learn will have higher fitness than those that do not ([Dunlap & Stephens 2009](#)). The real

ways. But *how* do animals learn? We examine that question in the next two sections. First, we look inside the brain to see proximate changes in neurons associated with learning. Then, we examine how animals learn by making associations.

## 7.2 Learning is associated with neurological changes

### Learning Objectives

After reading this section, you should be able to

- describe how neurotransmitter release is associated with learning,
- explain how the formation of dendritic spines is associated with learning, and
- describe the relationship between hippocampal formation size and memory of spatial locations in birds.

How are experiences translated into changes in behavior? In [Chapter 5](#), we saw how information from experiences and environmental stimuli is perceived via sensory receptors and relayed to the central nervous system through nerves. Recall that nerves are composed of neurons, cells that receive and transfer electrical and chemical signals. The junction between two neurons, the synapse, is believed to play an important role in learning and memory. Two aspects of the nervous system have garnered much attention in research on learning: changes in neurotransmitters and the number of synapses between neurons. One neuroethological approach to understanding such proximate mechanisms of learning is to characterize synapse characteristics before and after a learned experience to determine what changes occur. This is the approach used in the next two studies.

### FEATURED RESEARCH Neurotransmitters and learning in chicks

One important form of learning is **imprinting**, rapid learning that occurs in young animals during a short, sensitive period and has long-lasting effects. For example, offspring often learn the phenotype and identity of their parents through filial imprinting, because their parents are the first objects they encounter. Vulnerable offspring benefit from this learning by being able to quickly identify their parents and remain close to them. Konrad Lorenz made imprinting famous when he showed how graylag geese (*Anser anser*) hatchlings would imprint on his boots when these were the first objects they saw. In the absence of their parents, they simply followed him (his boots) around ([Figure 7.6](#)) ([Lorenz 1935](#)). More recently, this behavior has been used for the reintroduction of endangered birds to their former habitats ([Applying the Concepts 7.1](#)).

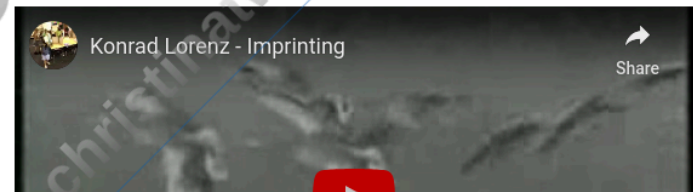


FIGURE 7.6. Lorenz and geese. A clutch of geese that imprinted on Lorenz's boots.

### Video: Konrad Lorenz and imprinting

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Video: Konrad Lorenz and imprinting



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## APPLYING THE CONCEPTS 7.1

### Operation Migration and imprinting

Many birds follow long migration routes from their summer breeding areas to their winter feeding grounds. Birds typically learn these routes from their parents. However, the hand-reared birds of endangered species that are being reintroduced into the wild do not have this option. How can they learn their natural migration routes? William Sladen and his colleagues hypothesized that imprinting could be used to train young birds to follow a human flying an ultralight aircraft ([Sladen et al. 2002](#)).

Work began with a common species, the Canada goose (*Branta canadensis*). The researchers took eggs from parents, hatched them in an incubator, and hand-reared them. Birds did indeed imprint on the human handlers and followed them as they flew the aircraft, first over short distances, but eventually over longer flights. The same procedure was then used to train endangered species raised in captivity, such as trumpeter swans (*Cygnus buccinator*) and whooping cranes (*Grus americana*) (Figure 1) ([Ellis et al. 2003](#)). This success is particularly impressive given the cranes' 1,800 km migration. This research inspired the movie *Fly Away Home*, in which captive Canada geese imprint on a young girl. She trains the birds to follow their historic migration route all the way from Ontario, Canada, to North Carolina. ■

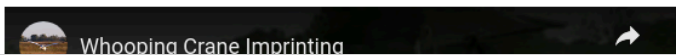


FIGURE 1. Imprinting on aircraft. Whooping cranes following an ultralight aircraft.

#### Video: Whooping Crane imprinting for migration

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Video: Whooping Crane imprinting for migration



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Many birds, like domestic chickens (*Gallus gallus domesticus*), visually imprint on a stimulus when they hatch. In their brain, the intermediate and medial parts of the hyperstriatum ventrale (IMHV) appear to play an important role in memory related to imprinting; earlier work demonstrated that lesions in this area of the brain prevent imprinting, as does the blocking of postsynaptic neurotransmitter receptors ([Hoern 2004](#)).

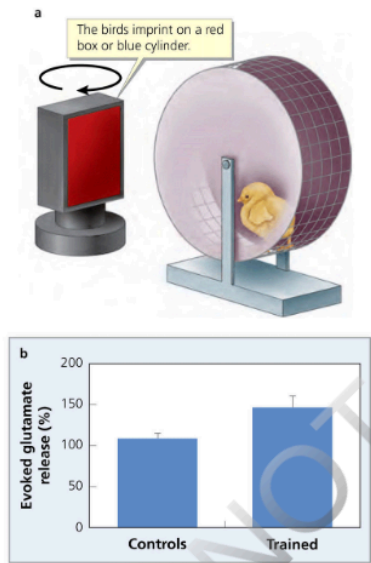
Rhiannon Meredith and her colleagues studied another imprinting mechanism in chicks by investigating whether the release of neurotransmitters from the presynaptic neuron is also associated with such learning ([Meredith et al. 2004](#)). The researchers divided chicks into two groups. Half were trained by exposure to a visual imprinting stimulus (a red box or a blue cylinder). The other birds were used as a control group and were given no visual stimulus for imprinting. During imprinting training, birds were placed on a running wheel; typically, they attempted to move toward the stimulus, and the wheel recorded these movements.

Less than ten minutes after training, the researchers measured the strength of imprinting, or preference score, by sequentially placing two objects in front of the chick while it was on the running wheel. One was the imprinted object, while the other was a novel object. The preference score was calculated by dividing the amount of running the chick did toward the imprinted object during a fixed period by the total amount of running in response to both objects. A score of 50 showed no preference for the imprinted object, while higher scores showed greater preference and a higher strength of imprinting. At the end of the experiment, chicks were sacrificed, the IMHV tissue was dissected, and assays were conducted to measure the release of several amino acid neurotransmitters, including glutamate and gamma-aminobutyric acid (GABA).

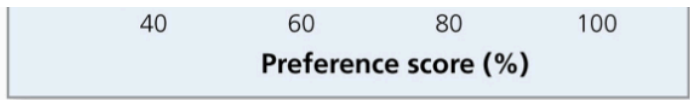
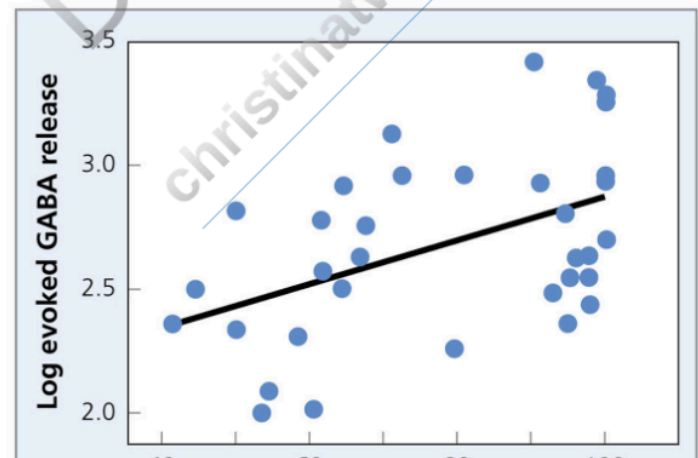
The research team found higher glutamate in the IMHV tissue of trained chicks compared to that of the controls ([Figure 7.7](#)), but no difference in GABA. However, among the trained birds, chicks with the highest preference score—those that most strongly imprinted on the test object—had higher levels of GABA in their brain ([Figure 7.8](#)). These results suggest that neurotransmitters play a role in imprinting. One neurotransmitter, glutamate, was more strongly released in the brain of birds that visually imprinted on an object, while another, GABA, was correlated with the strength of imprinting. This work illustrates that neurotransmitter release in presynaptic

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correlated with the strength of imprinting. This work illustrates that neurotransmitter release in presynaptic neurons played a role in imprinting over the short timescale of the experiment. Next, we examine recent research that investigates long-lasting memory.



**FIGURE 7.7. Glutamate release and training.** (a) Training protocol. (b) Mean (+ SE) glutamate release in different chicks. More glutamate was detected in trained than in control birds. (Source: [Horn 1998](#)) (Source: [Meredith et al. 2004](#))

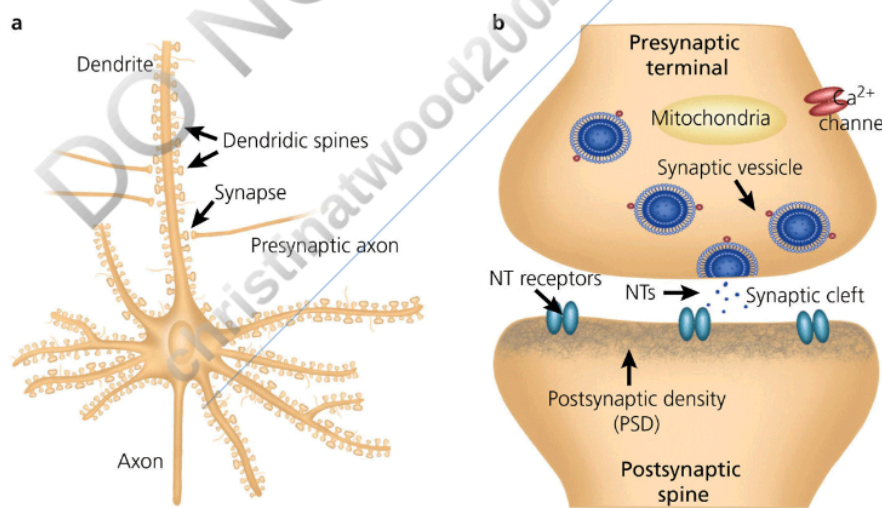


**FIGURE 7.8. GABA release.** Increased GABA was associated with higher preference scores (strength of imprinting). (Source: [Meredith et al. 2004](#))

## FEATURED RESEARCH Dendritic spines and learning in mice

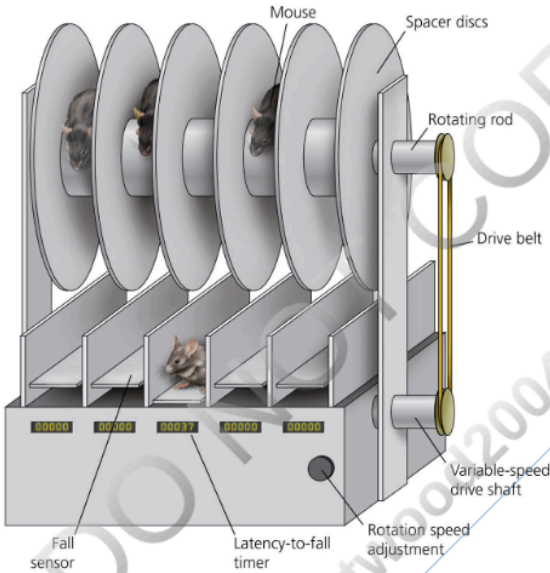
Memory is the retention of a learned experience. It is a critical factor in animals' ability to utilize their prior experiences. How is memory stored in the brain? Although we are just beginning to understand the answer to this question, changes in the brain appear to be involved.

Structural change in the brain, especially in the number of synapses and in the strength of chemical synapses between neurons, is a phenomenon known as neural plasticity ([Hering & Sheng 2001](#)). Synaptic connections in the brain are dynamic, owing partly to the formation and elimination of **dendritic spines**, small protuberances on a dendrite that typically receive synaptic inputs ([Figure 7.9](#)). The dynamic nature of dendritic spines means that the number of synaptic connections between neurons can vary. Recent work suggests that the dynamic nature of spines plays a role in learning.



**FIGURE 7.9. Neuron and dendritic spines.** (a) Dendritic spines are small protuberances on the dendrites of neurons in the brain. (b) Each spine forms a synapse with another neuron. NT = neurotransmitter. (Source: [Smti & Zhou 2010](#))

Guang Yang, Feng Pan, and Wen-Biao Gan examined spine formation associated with learning in mice (Yang, Pan, & Gan 2009). One group of mice was trained to learn a new motor skill: running on a rotating rod (a rotorod) suspended above the cage floor (Figure 7.10), an activity that is analogous to humans “logrolling” in water. The mice had to learn novel motor coordination skills and balance in order to stay on the rod as its speed increased. Another group of mice received no training and served as controls. The researchers used transcranial two-photon microscopy to examine the fluorescent-labeled dendritic spines of living subjects. This technique involves surgically thinning the cranium to allow for high-resolution imaging of dendritic spines.



**FIGURE 7.10. Rotorod.** Mice are placed on a rotating rod that increases in speed to develop a novel motor skill. Researchers measure the ability of mice to stay on the rod. (Source: Carter, Morton, & Dunnett 2001)

learning a new skill to evolutionary changes in brain structure associated with long-term memory. Next, we examine how animals learn by making associations.

**Video: Clark's nutcracker caching**

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**7.3 Animals learn associations between stimuli and responses**



## Learning Objectives

After reading this section, you should be able to

- distinguish classical from operant conditioning and provide one example of each and
- explain how learning curves are used in the study of operant conditioning.

Learning often requires making associations. For example, when we pick up a leash, our dogs associate that gesture with going for a walk. One common type of learning involves exhibiting a particular behavior when a certain stimulus is present—a stimulus–response association. Many animals make such associations, allowing them to learn about their environment, prepare for any similar future events, and respond accordingly.

## Classical conditioning

The researcher most often associated with stimulus–response learning is Ivan Pavlov. Pavlov was studying the physiology of digestion when he observed that dogs often began salivating when they could smell or see food. More interestingly, they would also begin salivating when they saw the technician who normally fed them. They had formed an association between the technician and the upcoming delivery of food ([Pavlov 1927](#)).

This ability to learn new associations between a stimulus and an innate, or unlearned, response is called **classical conditioning (or Pavlovian conditioning)**. Classical conditioning begins with an innate response to a stimulus, such as salivating in response to the sight of food. Pavlov called the food the unconditional stimulus (US) and salivating the unconditional response (UR). Next, he paired a neutral stimulus, such as the ringing of a bell, with the presentation of food. Such “conditioning” was done repeatedly until the animal learned to associate the bell with the arrival of food. In Pavlov’s terms, the bell was a conditional stimulus (CS), and salivation in response to the bell was a conditional response (CR). Subsequently, a dog would salivate after simply hearing the bell, even in the absence of food: a new predictable relationship had developed between a stimulus (bell) and a response (salivating). Often the word “conditioned” is used instead of “conditional” when referring to a stimulus or response. Next, we examine how such conditioning can affect fitness.

## FEATURED RESEARCH Pavlovian conditioning for mating opportunities in Japanese quail

Classical conditioning allows individuals to become better prepared for future events by learning new associations. How does such learning affect fitness? Elizabeth Adkins-Regan and Emiko MacKillop studied how classical conditioning affects mating behavior in Japanese quail (*Coturnix japonica*), medium-sized Asian birds commonly raised in captivity for egg production.

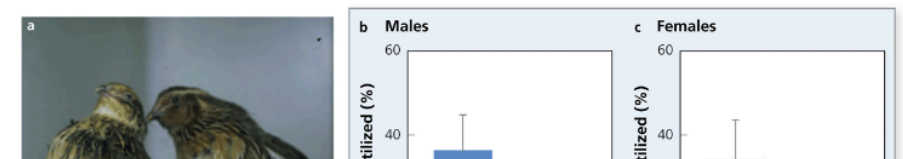
The researchers conditioned adult males and females in the laboratory to two different mating situations using cages that differed in size, location, and appearance (wire or Plexiglas construction) ([Adkins-Regan & MacKillop 2003](#)). Each bird learned that mating always occurred in one cage condition (conditioned stimulus, or CS+) but not the other (CS–) ([Figure 7.14](#)). For half the birds, a mate was added after two minutes only when they were placed in the Plexiglas cage, while for the other half, a mate was added only when they were in the wire cage. For the focal males, once the female was added, mating ensued. For females, no mating was allowed during conditioning, because female Japanese quails can store sperm, which could have biased the results. The male was thus kept behind a wire mesh screen. Training occurred twice a day for five days.

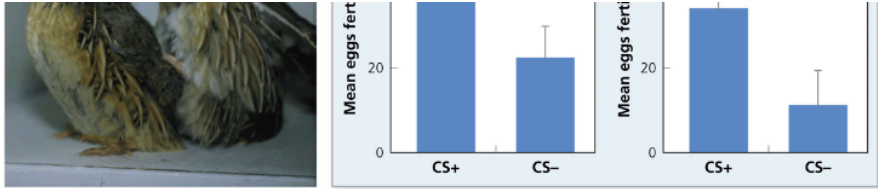
### Subjects:

6 males	cage A cage B	cage A (CS+)	cage B (CS–)	collection of eggs from test females	egg incubation	fertilization assessment
7 males	cage B cage A	cage B (CS+)	cage A (CS–)			
6 males	cage B cage A	cage B (CS–)	cage A (CS+)			
7 males	cage A cage B	cage A (CS–)	cage B (CS+)			
	1–5 (trials)	6 (test 1)	7 (test 2)	8–18	18–24	25
	Days					

**FIGURE 7.14. Conditioning design for males.** Cage A is made of wire and Cage B of Plexiglas. For training trials 1–5, mating only occurred in the CS+ cage (circled). During Tests 1 and 2, mating occurred in both cages. Females were given similar training but were not allowed to mate during training. (Source: [Adkins-Regan & MacKillop 2003](#))

After training, the focal individuals were tested in both cages: researchers presented these individuals with a mate and then counted the number of inseminations that occurred. Eggs were collected, incubated, and allowed to develop for one week before being examined for embryos. Males fertilized more eggs in the cage where they had been conditioned to expect a mate (the CS+ condition). Females also had more eggs fertilized in the CS+ condition ([Figure 7.15](#)). Both sexes thus achieved greater reproductive success in the condition where they had learned that mating opportunities occur.





**FIGURE 7.15. Percentage of eggs fertilized.** (a) A male copulating with a female. Mean (+ SE) percentage of eggs fertilized by (b) males and (c) females in the CS+ and CS- cages. (Source: [Adkins-Regan & MacKillop 2003](#))

These results show that Pavlovian conditioning can affect fitness. What caused these differences in fertilization success? The researchers hypothesized that males transferred larger or more effective ejaculates and that females behaved differently to allow more sperm transfer under the conditioned stimulus. Although the exact mechanism by which this occurred is not yet understood, it is clear that fertilization success was affected by the learning of conditions.

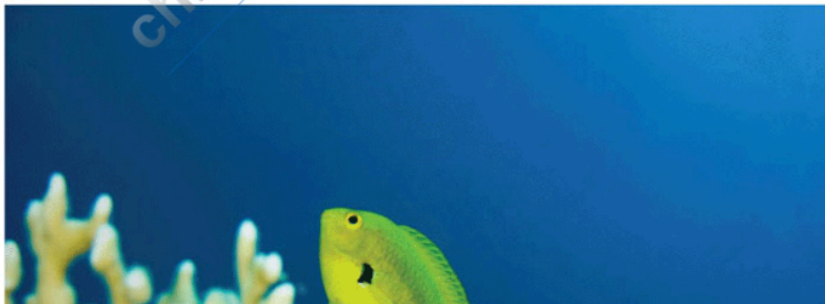
## FEATURED RESEARCH Fish learn novel predators

Another important component of fitness is predator avoidance. Many animals face the threat of predation, but how do they know to avoid predators? One possibility is that a prey can innately identify its predators. However, many animals move large distances when migrating or searching for appropriate habitats and so may encounter many different predators. Can they identify all possible predators innately, or do they learn about them?

Matthew Mitchell and colleagues examined the ability of juvenile lemon damselfish (*Pomacentrus moluccensis*) to learn about novel predators ([Mitchell et al. 2011](#)) ([Scientific Process 7.2](#)). Lemon damselfish larvae develop in open water for about a month, after which they settle on the Great Barrier Reef off the coast of Australia. Settlers are small (1 cm in length) and suffer high predation.

### SCIENTIFIC PROCESS 7.2

#### Fish learn predators



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Research Question: *How do fish learn about predators?*

#### Hypothesis:

Damselfish make associations between conspecific chemical alarm cues and the odor of a heterospecific fish to learn their predators.

#### Prediction:

Individuals will reduce feeding and increase antipredator behavior when they detect odors that have been associated with chemical alarm cues.

#### Methods:

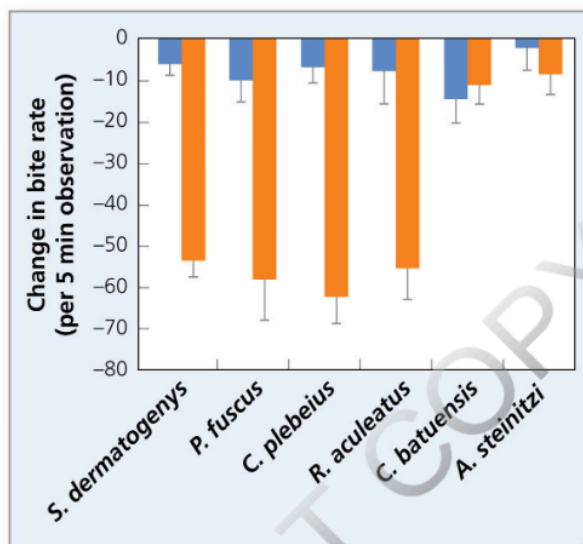
The researchers:

- Created two cocktails of odors: one from four species of known fish, A, B, C, and D (A = *S. dermatogenys*, a predator; B = *P. fuscus*, a predator; C = *C. plebeius*; D = *R. aculeatus*); and one from two species of novel fish, E and F (E = *C. batuensis*, a predator; F = *A. steinitzi*).
- Paired the cocktail with a conspecific chemical alarm substance (treatment)
- Paired the cocktail with seawater (control)
- Tested individuals by placing them in a 13 L flow-through tank with a shelter (a pot)
- Added food and recorded behavior for five minutes
- Added a stimulus odor (A–F) and recorded the amount of time test fish spent feeding, their distance from the shelter, and the time spent in the shelter for five minutes

#### Results:

Fish exposed to the cocktail plus the chemical alarm substance exhibited less feeding behavior than did control fish and fish exposed to a novel odor.

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**FIGURE 1. Feeding behavior.** Mean (+ SE) change in feeding behavior for treatment fish (orange) and controls (blue) when exposed to the odor of six fish species. From left to right, these represent fish A, B, C, D, E, and F. (Source: [Mitchell et al. 2011](#))

#### Conclusion:

Fish learn associations between the odor of a fish and chemical alarm substances.

#### Evaluate

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What data suggest that damselfish do not have an innate ability to detect a predator?

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Many fish, including damselfish, respond to conspecific chemical alarm substances released from damaged epidermal cells when, for example, a fish is wounded or killed by a predator. Fish that perceive chemical alarm substances respond with innate antipredator behaviors: they reduce feeding, increase vigilance behavior (scanning the environment for predators), and may spend more time in shelter. The researchers investigated whether fish learn their predators by association with the presence of the chemical alarm.

The experimenters created a "cocktail" of chemical odors using adults of four fish species caught from the reef: two fish predators and two nonpredators. They placed individuals of each species in separate tanks for six hours—enough time for the tank water to accumulate species-specific odors. The researchers then mixed water from each of the species' separate tanks to form the "cocktail" of chemical odors.

Mitchell's team next collected damselfish recruits that had not yet settled using traps set 50 to 100 m from the reef. Since predators of these fish are only found on reefs and not in open waters, the damselfish recruits were assumed to be naïve in regard to these predators. On Day 1, half the damselfish were conditioned to the cocktail odors plus a conspecific alarm substance. The other half were conditioned to the cocktail odors plus seawater as a control. The next day, damselfish were tested by exposing them either to odors from one of the cocktail species or to the odors of two novel species, only one of which was a fish predator. The researchers recorded the amount of time the test fish spent feeding, their distance from the shelter, and the time spent in the shelter.

When the odor of each species was added, damselfish conditioned with the cocktail of species and alarm substance reduced their feeding time significantly more than did the controls, although there was no difference in shelter use between the two groups. The test fish had apparently learned a new association between the odor of each cocktail fish and predation risk, as indicated by the chemical alarm substance. Individuals tested with the odor of the cocktail fish paired with seawater did not respond with antipredator behaviors. Individuals also did not respond to the odors of the two novel fish species, even though one was a predator.

These results demonstrate that lemon damselfish can rapidly learn associations between fish odors and the risk



these results demonstrate that damselfish can rapidly learn associations between non-food and the risk from unfamiliar predators, and can respond in an appropriate manner by reducing their feeding time. In addition, because damselfish did not respond to the odor of a novel predator, there was no evidence that they have innate knowledge of predatory species; instead, it appears they must learn to identify predators. The ability to make these important (and rapid) associations allows damselfish to minimize predation risk in new environments.

## Operant conditioning

As we just saw, classical conditioning involves learning novel associations that affect innate behavior. In contrast, **operant conditioning** involves learning associations between learned behaviors and outcomes. Charles Turner, Edward Thorndike, and B. F. Skinner pioneered the study of operant conditioning, also known as instrumental conditioning (Turner 1907; Thorndike 1911; Skinner 1938).

Through influential books, Skinner revolutionized the study of behavior in the mid-twentieth century (e.g., Skinner 1948), and his work is still used extensively to train animals (Applying the Concepts 7.2). From Skinner's perspective, much behavior is learned from the consequences of this conditioning. Any of four types of operant conditioning can occur, depending on whether a behavior becomes more or less likely as a result of the presentation or removal of a stimulus as follows:

1. In positive reinforcement, a behavior becomes more likely due to the presentation of a stimulus, such as food.
2. In negative reinforcement, a behavior becomes more likely due to the removal of a stimulus, such as pain.
3. In positive punishment, a behavior becomes less likely due to the presentation of a stimulus.
4. In negative punishment, a behavior becomes less likely due to the removal of a stimulus.

### APPLYING THE CONCEPTS 7.2

#### Dog training

Have you ever rung a friend's doorbell only to hear uncontrolled barking? Have you had a dog run full force at you through the front door? Dog owners face behavioral problems like these all the time. Usually the owner simply yells at the dog: "Get away from the door!" "Sit down!" "No!" or some other command that may be ineffective. Sophia Yin studied domestic animal behavior and used operant conditioning with positive reinforcement to train dogs with problem behaviors.

To address dogs' problems with greeting people, Yin and her colleagues turned first to professional dog trainers and guided them to train dogs to remain on a small mat for one minute, despite loud distractions (Yin et al. 2008). The trainers began with two exercises. First, the six dogs learned to eat from a remote-controlled food-reward dispenser. Once the dogs ate readily from the food dispenser, the trainers played a tone, which they followed by giving each dog a food reward. After the dogs learned to look for food after hearing the tone, the researchers added a condition: the dog had to look at the trainer before the food would be dispensed. In the second exercise, the dogs learned to walk toward a "target" and touch it with their nose, which again resulted in the tone and a food reward. Once the dogs had mastered these two exercises, the real training protocol began.

real training protocol began.

The protocol had three stages: (1) a "down-stay" on a rug-covered platform; (2) running to the platform and doing a down-stay; and (3) the down-stay with distractions (e.g., a doorbell, loud knocking, or people walking). Training sessions lasted up to 30 minutes, depending on the dog's motivation. The trainers taught the dogs to complete the behaviors for each stage separately and then put them together in sequence. After eight days in the laboratory, dogs remained in a down-stay for a full minute despite distractions, whereas before training, they did so for only five seconds.

Dog owners used these same techniques with similar success: barking decreased from 19 to two barks per minute, while jumping decreased from eight to almost zero jumps per minute after training. The authors concluded that positive reinforcement is a powerful technique for modifying dog behavior. Dog trainers and owners are using these same techniques all over the world (Miller 2001). ■

#### Video: Training your dog for good door manners

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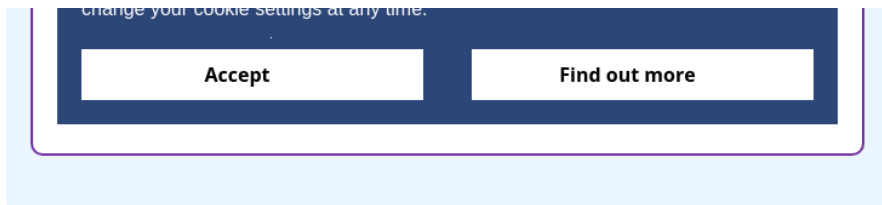
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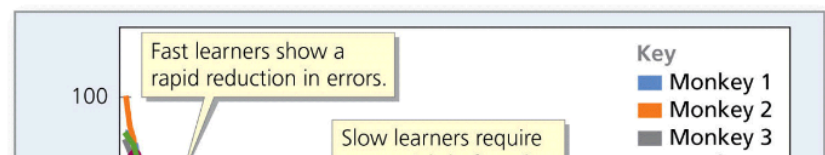
Much of Skinner's work involved understanding how and when each operant condition should be applied to produce the desired behavioral outcome. He also invented novel research protocols and apparatuses to study operant conditioning. A case in point is the operant chamber, or "Skinner box," which typically contains a lever that a rat or pigeon can press.

Operant chambers can be very useful tools to study animal problem solving. Operant conditioning is also known as **trial-and-error learning**, because behavior often changes incrementally as the animal "makes progress" toward solving a problem. Charles Turner first developed a graphical representation of such progress, such as a decline in errors over time, called the individual's **learning curve**; Skinner popularized their use. Learning curves allow researchers to quantify learning rate and characterize differences in learning ability, as we see next.

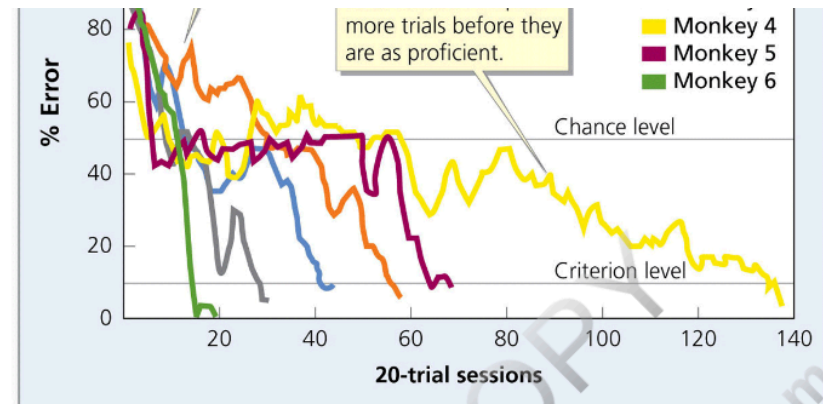
## FEATURED RESEARCH Learning curves in macaques

One way to understand how quickly animals learn is to train them to overcome an innate preference. For example, when given a choice between a small and a large quantity of food items, many primates, including humans, strongly prefer the larger quantity (Boysen, Berntson, & Mukobi 2001). This innate preference makes sense because food intake affects fitness, and so more is usually better. Elisabeth Murray, Jerald Kralik, and Steven Wise studied the strength of this preference in rhesus macaques (*Macaca mulatta*) (Murray, Kralik, & Wise 2005). They offered six subjects a choice between one or four peanut halves that were placed in the experimenter's open hands. If a test subject reached for the hand with one food item, it received four; when it reached for the hand with four food items, it received one. Here, one action provided four times more rewards than the other and therefore represented a more positive reinforcing outcome. Twenty trials were conducted each day, with a 20-second delay between them. How quickly did individuals learn to select the hand that contained only one food item?

As expected, each subject showed a strong initial preference for the hand with four food items (the "incorrect" but innate choice). Macaques did learn to select the hand with one food item in order to receive four, demonstrating trial-and-error learning, but there was tremendous variation in their learning curves (Figure 7.16). One macaque learned rather quickly, attaining a low error rate after about 340 trials, but another macaque took over 2,700 trials to attain a low error rate. In fact, a wide variation in learning curves is common in many species (Boutin 2007).



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**FIGURE 7.16. Macaque learning curves.** Individual macaques (different lines) learned to select the hand with one food item instead of the hand with four at different rates. Those macaques that learned the fastest had the fewest errors in the least number of trials. (Source: Murray, Kralik, & Wise 2005)

## FEATURED RESEARCH Trial-and-error learning in bees

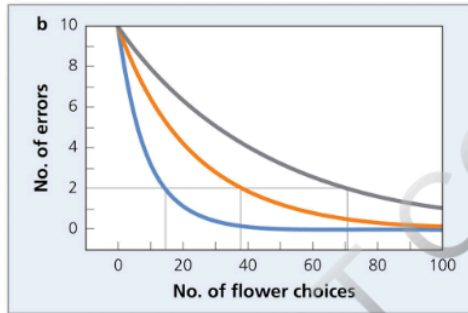
Following Skinner's work and the development of operant chambers, many learning studies, like the previously described work on macaques, were conducted in laboratory settings designed to control as many factors as possible. Can operant learning be studied in more natural settings? And, given that individuals differ in their learning rate, does learning ability affect fitness?

Nigel Raine and Lars Chittka set out to answer those questions (Raine & Chittka 2008). Bumblebees (*Bombus terrestris*) use a variety of cues to learn which flowers provide nectar and pollen food rewards. Bees feed on many types of flowers but have an innate preference for the color blue, because blue flowers tend to have more nectar (Raine & Chittka 2007). Using operant conditioning, Raine and Chittka examined the learning curves of bees trained to associate the color yellow with a food reward in the laboratory.

The researchers worked with 12 colonies that contained uniquely marked workers. All bees were first allowed to feed from artificial flowers that contained sugar water. Each flower was multicolored—both blue and yellow. Once bees were used to feeding from artificial flowers, the researchers began training trials. Bees were placed in a flight arena where half the artificial flowers were all blue and half were all yellow. Only the yellow flowers contained sugar water, whereas the blue flowers were empty. Thus, bees had to learn that they would be rewarded for probing yellow flowers and not for probing blue flowers.

The researchers recorded over 100 flower visits per bee as bees searched for food. At first, bees in all colonies made mostly incorrect choices because of their innate preference for blue flowers, but all eventually learned to select mostly yellow flowers. However, the colonies differed in their learning rate: some learned quickly, while others did so much more slowly (Figure 7.17).

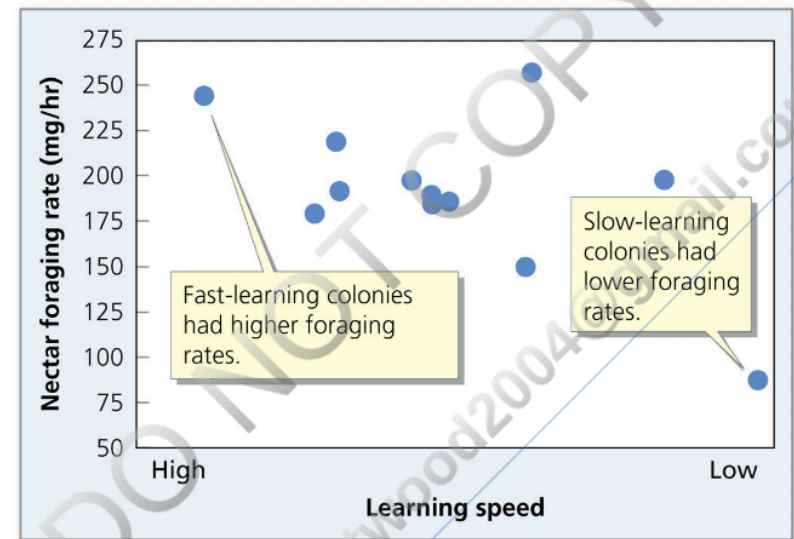
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**FIGURE 7.17. Bumblebee colony learning curves.** (a) Bumblebee foraging. (b) Average learning curves for bees from three colonies. Note the variation in learning rate among colonies. (Source: [Raine & Chittka 2008](#))

Next, the researchers investigated whether this variation in learning was associated with differences in fitness in

a natural environment. They allowed bees from each colony to forage on wildflowers around Queen Mary's College in London. They then measured foraging success based on a bee's weight when departing and its weight when returning to the hive, with the difference being the mass of nectar that the bee was bringing to the hive. Bees were allowed to forage naturally for six days, providing data from thousands of foraging bouts. Colonies differed in food delivery: those quick to learn in the laboratory delivered more food per hour to the colony than did slow learners, which researchers hypothesized would lead to enhanced survivorship ([Figure 7.18](#)). From these experiments, the researchers concluded that bees can learn where to feed by trial and error and that learning ability can affect fitness.



**FIGURE 7.18. Learning speed and feeding rate.** Mean nectar foraging rate for the 12 colonies. Colonies with a high learning speed in the experiment had higher mean feeding rates on wildflowers. (Source: [Raine & Chittka 2008](#))

These examples demonstrate that animals often learn by making associations. Many individuals may learn in isolation, as we saw in the work on Japanese quail. But in many species, individuals live with conspecifics, a situation that provides a rich social environment and enhanced learning opportunities, as we see next.

## 7.4 Social interactions facilitate learning

### Learning Objectives



After reading this section, you should be able to

- explain the benefit of social learning for an individual and
- describe the three criteria of animal teaching and provide one example.

In social species, other individuals are a source of information for learning, a phenomenon known as social learning. In individual learning, such as trial-and-error learning, information is acquired through an individual's own activities, while in social learning, individuals learn by observing others. Social learning can be favored by selection when it reduces the time and energy costs of learning (Rieucou & Giraldeau 2011).

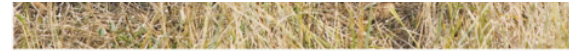
Young animals have much to learn about their environment, and for many species, one of the most important lessons is how to avoid being eaten. We begin with an example illustrating the benefits of social learning in this context.

## FEATURED RESEARCH Learned antipredator behaviors in prairie dogs

Many animals are highly vulnerable to predators. For example, black-tailed prairie dogs (*Cynomys ludovicianus*) are large social rodents that live in arid grassland habitats in North America (Figure 7.19) that also contain predators such as black-footed ferrets (*Mustela nigripes*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and a variety of hawks and rattlesnakes. How do young prairie dogs learn to avoid them?



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**FIGURE 7.19. Prairie dogs.** Highly social rodents that live in large colonies.

Debra Shier and Donald Owings tested the hypothesis that young prairie dogs learn antipredator behaviors from adults (Shier & Owings 2007). They captured 36 juveniles with their mothers within two days of emergence from their burrows. Each mother and her litter were housed in a separate enclosure with an artificial underground burrow at one end. Each juvenile first went through a pretraining assessment of antipredator behavior with predator test stimuli: a black-footed ferret, a prairie rattlesnake (*Crotalus viridis*), a moving hawk model, or a cottontail rabbit (*Sylvilagus audubonii*), which served as a nonpredator control. The ferret and rabbit were presented within a mesh box, the snake was presented behind a mesh barrier, and the model hawk was flown over the enclosure. The researchers filmed each juvenile for ten minutes to record its antipredator response to the test stimulus.

Next the young pups underwent a five-week training period in which they were randomly divided into two groups and exposed to the predators. One group spent five weeks with an experienced adult that had lived in the wild and had previous exposure to the chosen predators. The other group either trained alone or with an inexperienced sibling. Following training, juveniles were given a post-training test in which their response to each test stimulus was recorded when they were alone. The researchers measured the juveniles' activity level, frequency of fleeing, antipredator vocalizations, and vigilance behavior.

### Video: Prairie dog snake alarm

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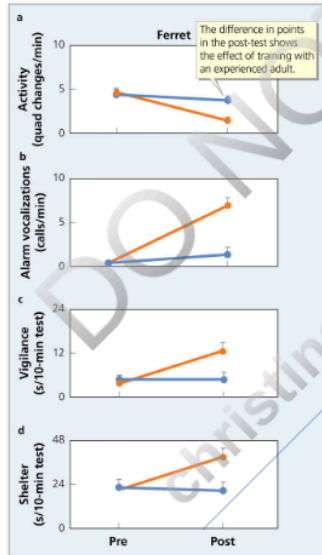


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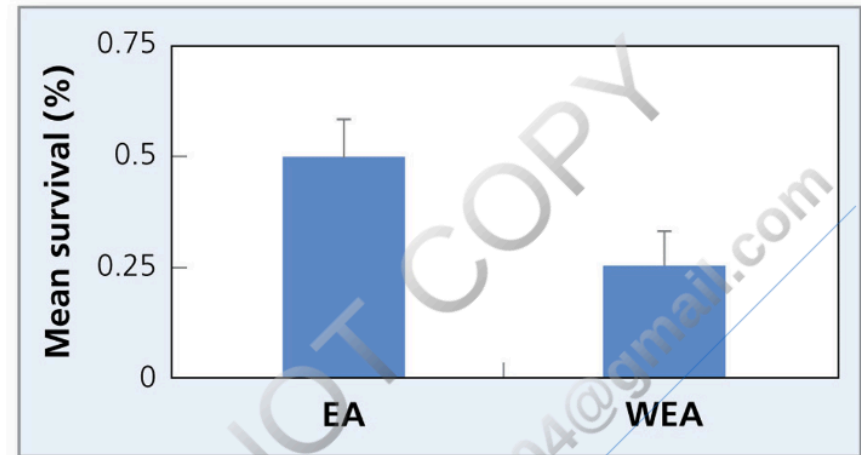
The post-training tests indicated that the treatments strongly affected antipredator behavior. Prairie dog juvenile pups trained with an adult were less active, produced more alarm calls, exhibited greater levels of vigilance, and more often fled to the burrow when exposed to a predator (Figure 7.20).



**FIGURE 7.20. Juvenile antipredator behavior.** Mean (+ SE) antipredator behavior of juveniles trained with an experienced adult (orange) and those not trained with an experienced adult (blue) for exposure to one predator type, a ferret. (a) Activity level, (b) alarm vocalizations, (c) vigilance rate, and (d) time in shelter before (pre) and after (post) training. Note large differences in behavior in the post-training data. (Source: Shier & Owings 2007)

Following these tests, all juveniles and adults were marked and released back into the wild in a new colony to assess their survivorship. One year after testing, the juveniles reared with experienced adults had higher

assess their survivorship. One year after testing, the juveniles reared with experienced adults had higher survivorship (Figure 7.21) than those reared alone or with inexperienced siblings. Shier and Owings concluded that juveniles learn antipredator behaviors from experienced adults and that learning helps them survive. Interestingly, social learning may play a role in how human children learn about dangerous animals (Applying the Concepts 7.3).



**FIGURE 7.21. Survivorship differences.** Mean (+ SE) survival probabilities. Juveniles trained with an experienced adult (EA) had higher survivorship in the wild after one year than juveniles trained without an experienced adult (WEA). (Source: Shier & Owings 2007)

### APPLYING THE CONCEPTS 7.3

#### Human social learning about dangerous animals

Prairie dogs and many other animals learn about predators through social learning (Griffin 2004). H. Clark Barrett and James Broesch tested the hypothesis that human children also learn socially to remember the relative danger posed by different species (Barrett & Broesch 2012).

The researchers conducted a simple experiment using children under the age of 12 from one urban area (Los Angeles) and one rural area (a Shuar village in the Amazon region of Ecuador). In each societal group, half the children were assigned to the social learning treatment and half were assigned to the control (no learning). Each child was shown individual images of 16 different animals on cards. The species depicted came from several different continents and were largely unfamiliar to most of the children prior to the study.

To gauge the ability to infer level of danger or an animal's diet from the images, the control children were asked a series of questions about each card. In the social learning treatment group, the experimenter told the children each animal's common name, whether it ate plants or animals, and whether it was "dangerous" or "safe." The cards were then shuffled, and each

animals, and whether it was “dangerous” or “safe.” The cards were then shuffled, and each image was shown again, but this time the experimenter asked the children to repeat the information. To assess longer-term learning, this procedure was repeated one week later.

Few of the children could correctly name any of the animals depicted on the cards, and the children performed poorly on this task both immediately after learning the names and one week later. In addition, both control and treatment children performed poorly when asked about a species’ diet, answering correctly only about 50% of the time. However, children who had been informed about the level of danger of each animal performed significantly better on the question about danger than control children, both immediately after learning this information and one week later. Shuar and U.S. children performed similarly on the task. These data suggest that human children can learn socially about animals and the level of danger they present. ■

In addition to avoiding predators, animals need to find food to survive and reproduce. In the next example, we see how social learning facilitates learning about food patches.

## Learning about food patches

Birds such as terns feed on fish near the water’s surface by diving into the water. Their food patches—schools of fish—are always moving, which can make locating food especially challenging. Individuals will often use a strategy known as **local enhancement**, in which they look to other foraging individuals as a cue to the location of food. This phenomenon is an important aspect of social learning.

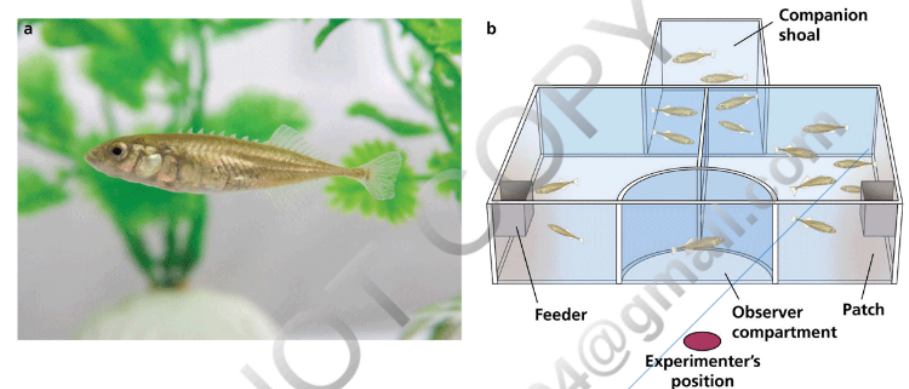
Location, however, is only one aspect of a food patch. Perhaps even more important is the quality of that patch, or how much food it contains. How can an individual learn about food patch quality? One possibility is again local enhancement. The more food a patch contains, the more foragers will typically be present at that patch. An even better strategy for determining patch quality is to observe individual feeding rates in a patch. Feeding rates will be high in rich patches and low in poor patches. Knowledge obtained from others about the quality of a resource is called **public information**, which can improve an individual’s assessment of resource quality (Valone 1989).

## FEATURED RESEARCH Social information use in sticklebacks

Do animals use public information to assess patch quality? Isabelle Coolen and her colleagues examined this question in nine-spined sticklebacks (*Pungitius pungitius*), small fish that live in lakes and rivers throughout the Northern Hemisphere (Coolen et al. 2005). They predicted that if only local enhancement information is available, individuals will use it, because high numbers of fish should indicate the best patch. If fish can observe the feeding success of others, however, they should use that public information to select a food patch—regardless of the number of fish at the patch.

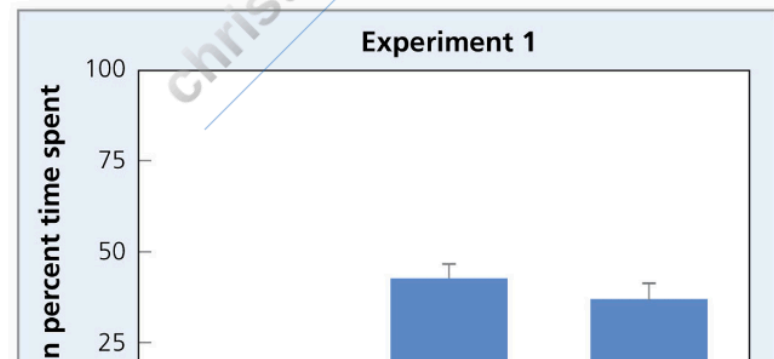
To test this prediction, the researchers divided a tank into three areas (Figure 7.22). Each side compartment contained a feeder, creating a “food patch.” The center area contained a compartment with a single observer, the test fish. In a first experiment, a test fish could see conspecific “demonstrators” at each food patch. Six

demonstrators were at one food patch, and two were at the other. Across from the test fish were six conspecifics viewed through a one-way mirror. The conspecifics served as a “companion shoal” so that the test fish was never isolated, even when the demonstrators were removed. No food was provided from either feeder, so only local enhancement information was available—the number of demonstrators. After ten minutes, the barriers and all demonstrators were removed and the observer was allowed to swim freely in the entire tank, although no food was actually present. The researchers recorded the mean percentage of time the test fish spent in each compartment and at the center near the companion shoal.

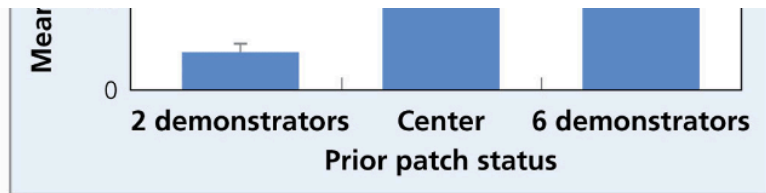


**FIGURE 7.22. Stickleback experimental tank.** (a) Stickleback. (b) Test aquarium. Individual test fish were placed in the observer compartment. Two or six demonstrators were placed in each side compartment, which contained a food patch, the feeder. The companion shoal of six individuals did not have access to food during demonstrations. (Source: Coolen et al. 2005)

The test fish spent significantly more time at the patch that had previously contained six demonstrators and near the central compartment than in the compartment with only two demonstrators (Figure 7.23). Sticklebacks were apparently using the number of fish at each food patch as a cue to its quality.



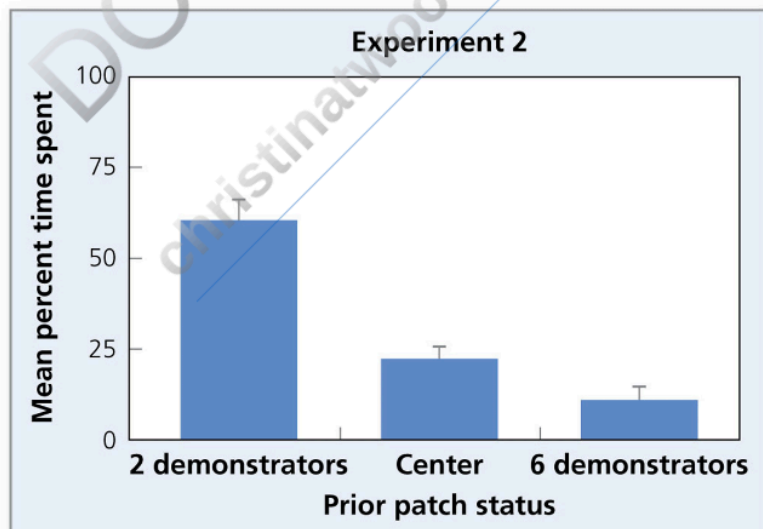




**FIGURE 7.23.** Percentage of time in each patch when seeing demonstrators that do not feed. Mean (+ SE) percentage of time spent in different locations. When demonstrators did not feed during the observation period, test fish spent more time near the patch that had six demonstrators compared to the patch that had only two demonstrators. (Source: Coolen et al. 2005)

To determine whether sticklebacks also use public information to estimate patch quality, the researchers conducted a second experiment in which they manipulated the feeding rates of demonstrators at each patch. The experimental tank was the same as before, but now the test fish could watch demonstrators feed on bloodworms from each patch. The patch with two demonstrators was designated the “rich” patch, and food was released from the feeder there six times during the ten-minute trial. The patch with six fish was designated the “poor” patch, and food was released there only twice during the trial. Feeding rates therefore differed at the two patches.

After all demonstrators and food were removed, the test fish exhibited a strong preference for the rich patch, even though only two fish had been there (Figure 7.24). Coolen’s team concluded that fish do use public information to select a patch. When local enhancement and public information provide contradictory information, as they did in the second experiment, fish rely on public information to select a food patch, likely because it provides more accurate information about patch quality.



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**FIGURE 7.24.** Percentage of time in each patch when seeing demonstrators that feed. Mean (+ SE) percentage of time spent in different locations. When feeding rates of demonstrators differed during the observation period, test fish spent more time at the rich patch that had two demonstrators compared to the poor patch that had six demonstrators. (Source: Coolen et al. 2005)

In the cases discussed, individuals learned how to avoid predators or about the quality of food patches by observing others. Such learning by observation is common and requires no special effort on the part of the demonstrators. Recently, however, evidence suggests that some demonstrators play a more active role in the social learning process—a phenomenon known as teaching.

## Teaching

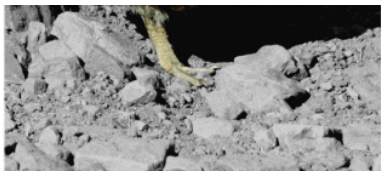
The hallmark of **teaching** is the active participation of an experienced individual in facilitating learning by a naïve conspecific. Animal teaching has been defined in many ways, but three widely accepted criteria for evidence of teaching are (1) one experienced individual, the teacher, modifies its behavior only while in the presence of a naïve pupil; (2) the behavior is costly for the teacher; and (3) the pupil acquires knowledge or a skill more rapidly through the actions of the teacher than it would otherwise (Caro & Hauser 1992). Let’s examine two cases that satisfy these criteria.

## FEATURED RESEARCH Ptarmigan hens teach chicks their diet

Some birds, like chickens, are precocial, or highly developed and mobile when they hatch, and so quickly need to learn what to eat. Jennifer Clarke examined how precocial white-tailed ptarmigan (*Lagopus leucura*) (Figure 7.25) chicks learn their diet (Clarke 2010). In particular, she investigated whether hens taught their chicks what to eat.



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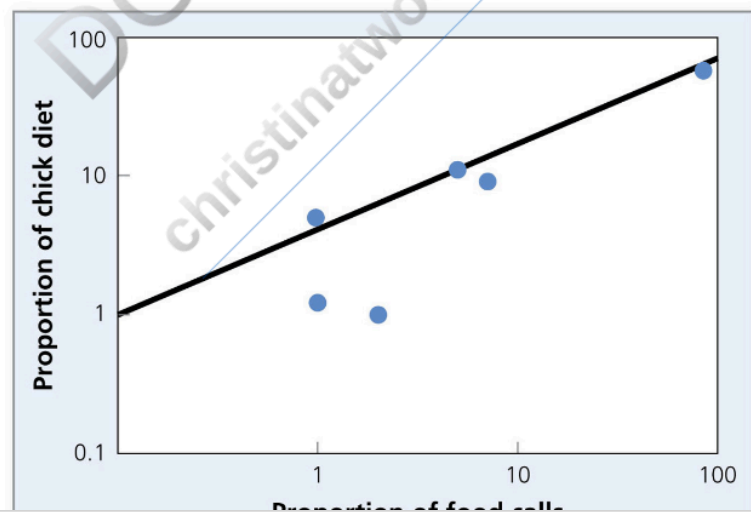


**FIGURE 7.25. White-tailed ptarmigan.** A common bird in alpine meadows in western North America.

Ptarmigans feed on a variety of leaves, flowers and buds, and berries of shrubs and wildflowers. Their natural habitat contains many dozens of plants, but the diet of ptarmigans is composed of just a small subset of available plants. How do chicks learn the plants (and plant parts) to eat? Chicks follow hens for several weeks after hatching. Occasionally, when one or more chicks are nearby, a hen will drop bits of food it is eating, produce a unique vocalization (a food call), and bob its head up and down. In response to this food call display, nearby chicks will run to the hen and feed. Are these displays a form of teaching?

Clarke observed seven marked hens and their chicks in over 100 feeding bouts and noted all food call displays that occurred. In these bouts, she recorded the food items eaten by hens and chicks, the food plant associated with each food call display, and the behavior of the chicks in response to the call.

While hens fed on over a dozen species of plants, they produced food calls in association with only six. Food call displays always resulted in chicks feeding on the plant the hen had been feeding on, and there was a positive correlation between the proportion of food calls associated with those species and the proportion of food in the diet of the chicks (Figure 7.26). Biochemical analyses of the plants consumed by the chicks indicated that they were significantly higher in protein content than a random mixture of plants available in the environment. Protein is a limited but important nutrient for growing chicks (Scott, Holm, & Reynolds 1963).



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## Proportion of food calls

**FIGURE 7.26. Hen food call frequency and chick diets.** The proportion of food calls given by hens to each of six plant species and the proportion of those plants in the diet of chicks. The axes are logarithmically scaled. (Source: Clarke 2010)

Clarke also noted variation in the food calling behavior of the hens studied and in the food their chicks consumed. Chicks of hens that produced the greatest number of food call displays consumed significantly more protein in their diet than chicks of hens that produced the fewest food call displays. Clearly, hens were biasing food call production to plants high in protein, and chicks learned to consume a diet high in protein. These data are consistent with the definition of teaching, although the cost of teaching to the parent was only inferred (a reduced feeding rate).

Some argue that clear evidence of teaching requires an additional criterion: a modification in behavior by the teacher based on variation in learning by the pupil. In other words, evidence that the teacher modifies its behavior when the pupil is not learning. Let's examine one such case in ants.

## FEATURED RESEARCH Tandem running in ants

Social insect colonies provide much opportunity for social learning by individuals. *Temnothorax albipennis*, an ant common throughout Europe, lives in small colonies that often contain fewer than 100 workers (Dornhaus et al. 2008). Colonies are located in loose rubble or small rock crevices, and when these sites become unsuitable, colonies often move to more stable, higher-quality locations. A small number of scouts are always searching the environment for food or better nest locations. When a valuable resource is located, the scout returns to the nest to recruit additional workers. Recruitment takes the form of a tandem run (two individuals moving together) in which the experienced scout physically leads the naïve worker to the resource. Is this behavior a form of teaching?

Nigel Franks and Tom Richardson studied tandem running in ants housed in artificial nests in the laboratory (Franks & Richardson 2006). They used 1 m arenas with the nest at one end and a food source located at the other. Franks and Richardson recorded the movements of eight independent tandem runs, including the movement of the first scout to find the food, its behavior while engaged in tandem running with a naïve recruit, and the movement of the recruit back to the nest.

### Video: Teaching tandem running in ants

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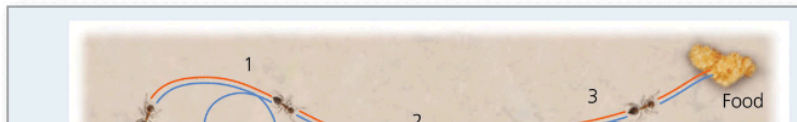
Video: Teaching tandem running in ants. A successful scout emits a pheromone signal to attract a follower. Followers indicate their presence through continuous antennal contact which the scout waits for.

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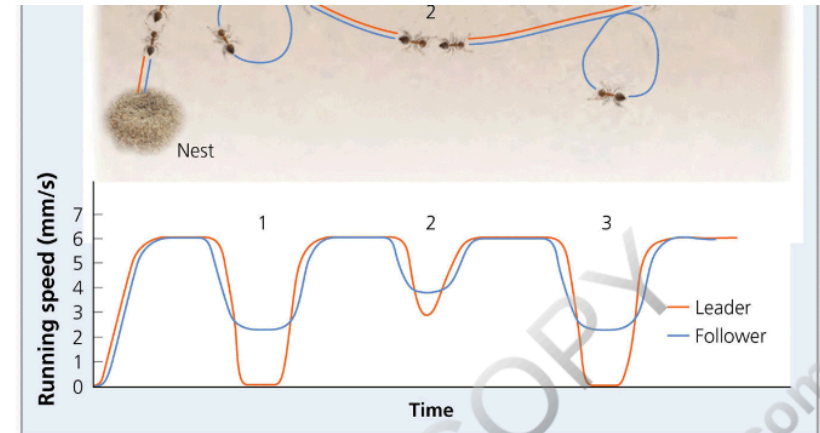
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Frame-by-frame analysis indicated that leaders moved toward the food when the follower maintained antennal contact by tapping on the legs and body of the leader. Occasionally, the recruit would break away from the leader and engage in a circuitous movement, perhaps acquiring visual information about the environment to learn the route it was traveling. When physical contact was broken, the leader would slow down or stop moving until the follower was again close enough to maintain contact (Figure 7.27). Slowing down to wait for the recruit meant that tandem runs were costly for the leader—it took four times longer for the leader to move between the nest and food when engaged in a tandem run. However, recruits engaged in a tandem run located the food significantly faster than naïve scouts: they benefited from the behavior of the leader. In addition, Franks and Richardson found that followers would subsequently become leaders for new recruits.



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**FIGURE 7.27. Tandem running ants.** (a) Schematic paths of leader (orange) and follower (blue) from the nest to food. (b) Associated running speeds of each ant making each path. The leader occasionally stops (Points 1 and 3) or slows (Point 2) to wait for the follower. (Source: Leadbeater, Raine, & Chittka 2006)

Tandem running behavior satisfies all three primary criteria for teaching. Furthermore, leaders modify their behavior in response to the behavior of followers in such a way that facilitates learning, and the information that followers learn allows them to later become tandem leaders/teachers themselves. This demonstrates that teaching behavior is not limited to vertebrates.

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These examples illustrate how social interactions between individuals can promote learning of a diverse array of behavior in both juveniles and adults. Next, we examine one outcome of social learning: the development of animal traditions and culture.

## 7.5 Social learning can lead to the development of animal traditions and culture

### Learning Objectives

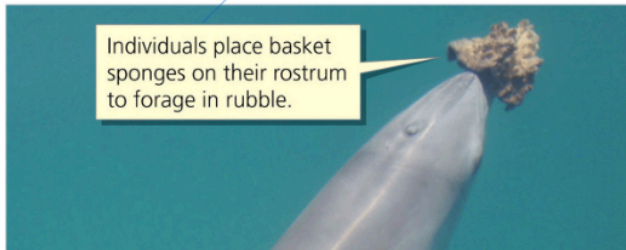
After reading this section, you should be able to

- identify behavioral traditions and
- explain evidence of a behavioral tradition in great tits.

We have seen that conspecifics can facilitate learning because they act as a source of information, and that such learning is beneficial, so social learning is widespread. Social learning can also lead to variation among populations. Among populations, differences in behavior that are transmitted between generations through social learning are called **behavioral traditions**.

One type of behavioral tradition commonly observed in populations of birds and cetaceans (whales, porpoises, and dolphins) are local song dialects, characteristic differences in songs that vary geographically. Song is learned from an adult tutor (as we saw in [Chapter 4](#)), and so changes can spread rapidly through different populations (e.g., [Noad et al. 2000](#); [Wright, Dahlin, & Salinas-Melgoza 2008](#)).

Another example of a behavioral tradition involves tool use. Bottlenose dolphins (*Tursiops* sp.) off the coast of Australia remove marine sponges from the substrate and wear them on their rostrum or beak as they probe the seafloor to locate submerged prey in rough rubble ([Figure 7.28](#)). Sponge tool-use behavior is found only in one population of dolphins near Shark Bay and tends to be most commonly observed in females. Do calves learn this behavior through social learning?



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**FIGURE 7.28. Dolphin tool use.** Dolphins use marine sponges to dig up hidden prey on the seafloor, which is strewn with sharp rubble.

Janet Mann and her colleagues used 14 years of data on the behavior of mothers and their calves to examine this question. They found that this behavior appears to be transmitted primarily from mothers to their offspring, suggesting that social learning plays a role ([Sargent & Mann 2009](#)). Further work indicates that sponge tool-use behavior may function to minimize damage to the skin while probing the rocky substrate for prey ([Patterson & Mann 2011](#)).

Chimpanzees also exhibit behavioral traditions involving tool use ([Figure 7.29](#)). For example, populations vary in their use of stones to crack nuts, their use of twigs to fish for termites, and in specific grooming and courtship behaviors ([Whiten et al. 1999](#)). Differences in multiple traditions may be evidence of broader differences among populations, or **animal culture** ([Whiten & van Schaik 2007](#)). Why do these differences among populations exist? One explanation might involve genetic differences. Alternatively, the variation across populations might correspond to ecological differences, because behavior that is adaptive in one environment might not be adaptive in another. Or differences among populations might exist due to ecological constraints. For instance, the use of stones to crack nuts requires the presence of both nuts and appropriate stones. If either is absent, the behavior will also be absent. A final possibility involves social learning, which could allow a trait to spread rapidly through one particular population, resulting in populations that differ in their behavioral traits. One way to test genetic, ecological, and social learning explanations for behavioral traditions and cultural differences is through experimental manipulation of populations, as we see next.



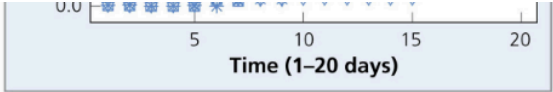
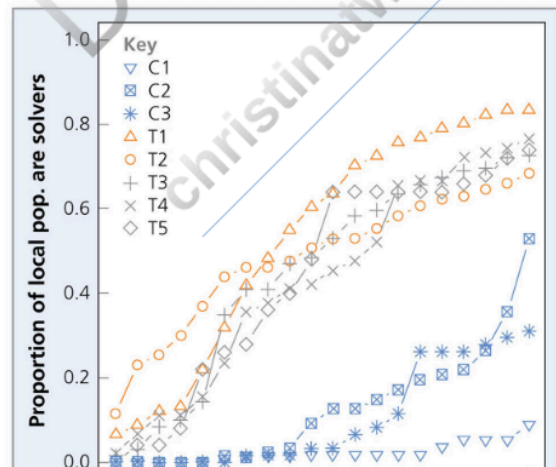
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**FIGURE 7.29. Tool use.** Wild bearded capuchin monkeys use stone tools to obtain food.

### FEATURED RESEARCH Foraging behavioral traditions in great tits

Lucy Aplin and her colleagues investigated the spread and persistence of a novel foraging technique in wild great tits (*Parus major*) to determine if it could be a behavioral tradition (Aplin et al. 2015). The experiment was conducted in eight subpopulations of birds that use nest boxes for breeding, so most birds had been captured and uniquely marked with a passive integrated transponder (PIT) tag. From each population, two males were captured. The males from five of the subpopulations were trained to open a puzzle box to obtain food (mealworms) by sliding a door either left or right: the males from two groups were trained to slide the door to the left (T1 and T2), while the males from three other groups (T3–T5 in Figure 7.30) were trained to slide it to the right. The males from the three remaining subpopulations served as controls (C1–C3) and received no training with the puzzle box. After four days of training, all the birds (“trained” demonstrators and untrained controls) were returned to their subpopulations, and three puzzle boxes were established in the local environment.



**FIGURE 7.30. Behavioral tradition in a feeding behavior.** The spread of problem solving for treatment subpopulations with trained demonstrators and control subpopulations without demonstrators. (Source: Aplin et al. 2015.)

Each puzzle box contained a PIT tag reader, motor, and circuit board, so the research team could determine the identity of an individual on the puzzle box and whether it obtained food by sliding the door left or right. The door reset one second after a solving bird had fed and departed. Data were collected over 20 days, at which time the boxes were removed. Nine months later, the boxes were reestablished in three of the subpopulations (one control, and one left-solving and one right-solving population) and the behavior of birds on the boxes was again recorded.

#### Video: Great tit research at Wytham Woods

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In each subpopulation with trained demonstrators, knowledge about how to obtain food from (i.e., solve) the puzzle box spread rapidly through the population over 20 days. Dozens of individuals in these subpopulations solved the puzzle box and tended to use the same technique (i.e., most birds in a subpopulation used a single technique). In addition, these solvers tended to be individuals that spent much time near one of the trained demonstrators, suggesting a role for observational learning to explain the rapid spread of the novel foraging technique in the population with a trained demonstrator. As such, birds in subpopulations learned the solutions used by their populations' trained demonstrators, an example of a behavioral tradition. In contrast, relatively few individuals in the control subpopulations learned to obtain food (Figure 7.30).

Nine months later, despite the natural turnover in all populations due to mortality, immigration, and reproduction, knowledge about how to obtain food from a puzzle box spread rapidly in the two populations that previously had trained demonstrators, and most birds again used the same technique (slide door left or right) that the original birds demonstrated. Again, few individuals in the control populations learned to obtain food.

These results show that a novel foraging technique—sliding a door either left or right to obtain food—can rapidly spread through a population through observations (social learning), and that such a behavioral tradition can persist over multiple generations. In addition, both ecological and genetic explanations for subpopulation differences in behavior can be rejected: all subpopulations had similar conditions (the puzzle boxes) and the population differences developed within a single generation.

In the last section of the chapter, we examine variation in the cognitive abilities of animals.

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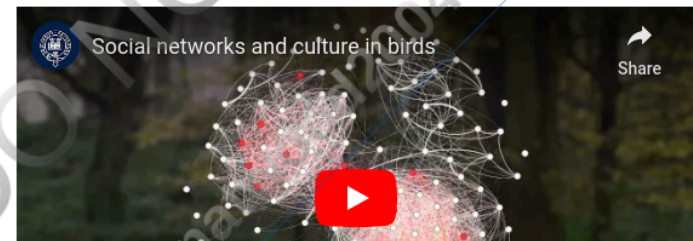
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In the last section of the chapter, we examine variation in the cognitive abilities of animals.

## 7.6 Animals vary in their cognitive abilities

### Learning Objectives

After reading this section, you should be able to

- identify animal cognition;
- describe how tool use, insight learning, and numerical competency are used to assess the cognitive ability of animals; and
- explain the cognitive buffer hypothesis and compare the evidence for it in birds and guppies.

There is a long history of interest in understanding the relative cognitive abilities of species. **Cognition** is broadly defined as the acquisition, storage, retrieval, and use of information for decision making ([Shettleworth 2001](#)) and usually is applied to learning that involves more than basic associations. Cognitive ethologists have used many approaches to study the cognitive abilities of animals, including those that focus on tool use, problem solving, numerical abilities, spatial memory, and self-recognition ([Pearce 2008](#)). Such studies have documented variation in performance on different cognitive tasks among individuals and across species (e.g., [Thornton & Lucas 2012](#)). Next, we examine how researchers have studied tool use, problem solving, and numerical abilities to understand the cognitive abilities of different species.

## FEATURED RESEARCH Tool use in capuchin monkeys

The ability to use tools is one aspect of cognition. As discussed earlier, many species use tools to acquire food that otherwise would be unavailable. Examples include sticks used by chimpanzees, finches, and crows to probe holes to feed on hidden insects; stones used by primates to crack open nuts; and, as we saw earlier, even sponges used by dolphins to feed on fish hidden in sharp rubble on the ocean floor ([Seed & Byrne 2010](#)). Selection can favor tool use when it enhances foraging ability.

In many cases, individuals learn to use a tool by trial and error after having observed others (e.g., [Lonsdorf 2005](#)). But some species appear capable of understanding the problem to be solved by the tool and then discover a functional solution without trial-and-error learning. One approach to understanding this enhanced cognitive aspect of tool use is to examine how individuals select a tool to solve a problem.

Elisabetta Visalberghi and her colleagues experimentally examined how bearded capuchin monkeys (*Cebus libidinosus*) selected stones to use as hammers to open nuts ([Visalberghi et al. 2009](#)). Wild capuchins at a study site in Brazil naturally use stones to open palm nuts. Typically a nut is placed on a log and a stone is dropped on the nut to open it. Success in obtaining food requires the use of heavy stones that will not fracture during use. At the study site, all stones made of sandstone are too fragile while stones composed of harder quartzite less than 200 g in size are too light to be used successfully: only heavy quartzite stones make effective hammers to open palm nuts. Can capuchins select the correct stones?

### Video: Capuchins using tools

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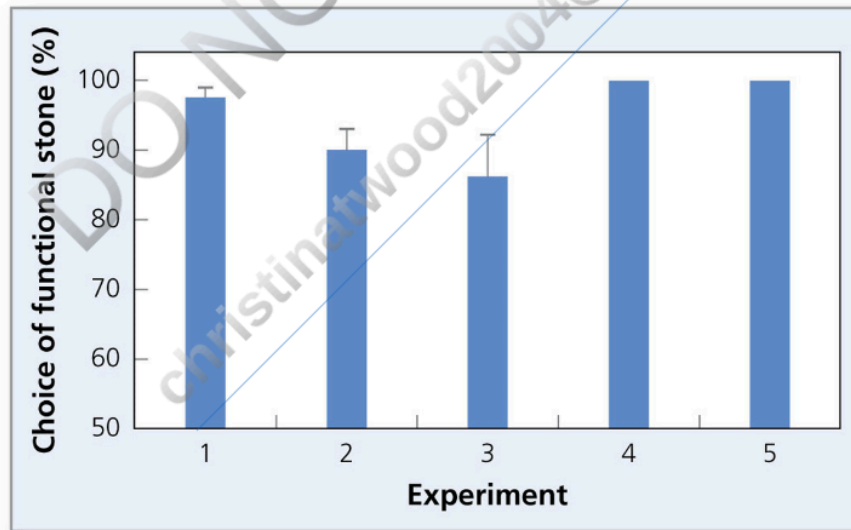


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The experiment consisted of providing eight different individuals with a palm nut at a log and a choice of stones supplied by the researcher after all natural stones were removed from an area. The first two experiments (Experiments 1 and 2) offered natural stones that differed in type (sandstone or quartzite) or varied in size and weight (large and heavy versus small and light quartzite). The research team recorded the first stone touched, the stone transported to the log and used to hit the nut, and the individual's success at obtaining food. All individuals were tested ten times in each experiment. Capuchins overwhelmingly selected the functional stone: the quartzite and heavier stone were selected in over 90% of the trials ([Figure 7.31](#)).

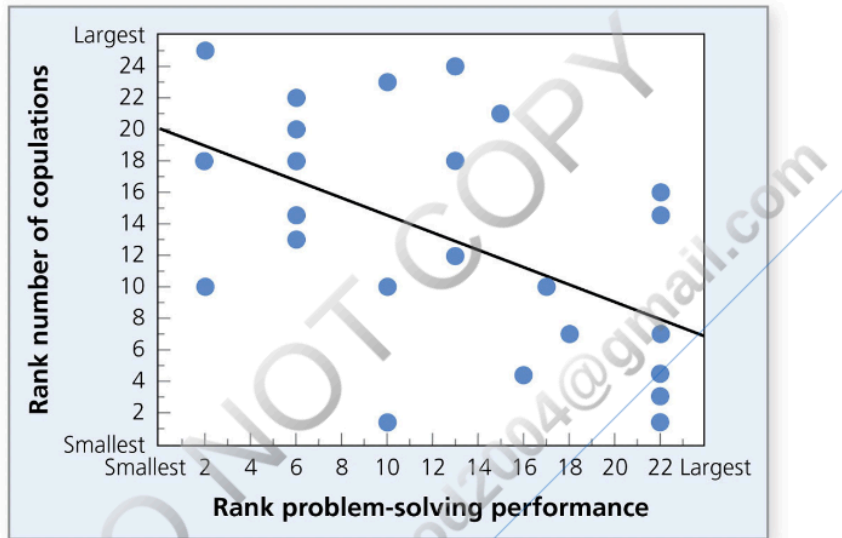


**FIGURE 7.31. Capuchin stone tool choice.** In five experiments (1–5) that provided one functional and one nonfunctional stone tool, capuchins overwhelmingly selected the functional stone. (Source: [Visalberghi et al. 2009](#))

In the next three experiments, the research team offered capuchins novel artificial stones whose weight did not correlate with size (a condition not typical in nature). Individuals were offered two stones that were the same size but differed in weight (Experiment 3); two stones that were either light and large or heavy and small (Experiment 4); and three stones that were light and small, light and large, or heavy and large (Experiment 5). All these novel stones were made of the same material and so only differed in the properties described.

For the novel stones in which size and weight were uncorrelated, capuchins again overwhelmingly selected the functional stone ([Figure 7.31](#)), but did so

There was a strong relationship between these variables: males with high problem-solving ranks (shortest time to solve the problem) tended to have the highest number of copulations (Figure 7.39). These data suggest an association between cognitive performance (problem-solving ability) and fitness for male satin bowerbirds and so support the cognitive performance hypothesis. Why such males were more attractive to females is unclear. One possibility is that problem-solving ability may correlate with other factors females use to select mates, such as a male's ability to obtain colorful decorations for his bower.



**FIGURE 7.39. Cognitive ability and copulations.** Individuals that tended to solve the problem quickly (small rank problem-solving performance) also tended to copulate with the most females (high rank number of copulations). (Source: [Keagy, Savard, & Borgla 2009](#))

These examples illustrate that animals vary in their cognitive abilities. Continued studies of tool use, insight learning, and numerical competency will continue to provide different avenues to understand the mental capacities of animals and the evolution of cognition.

## CHAPTER REVIEW

- |  |   |
|--|---|
| <p><b>7.1 Learning allows animals to adapt to their environment</b></p>                        | <ul style="list-style-type: none"> <li>• Learning is a process by which animals modify their behavior, through experience, in ways that allow them to experience increased fitness.</li> <li>• Salamander neonates rapidly learned to forage in a more efficient manner as they gained experience.</li> <li>• Fiddler crabs learn to habituate to a nonthreatening moving object.</li> </ul>                              |
| <p><b>7.2 Learning is associated with neurological changes</b></p>                             | <ul style="list-style-type: none"> <li>• In chicks, the release of neurotransmitters such as glutamate from the presynaptic neuron is associated with learning.</li> <li>• Neural plasticity, including the formation and elimination of <b>dendritic spines</b>, is associated with learning in mice.</li> <li>• In birds, hippocampal formation size in the brain correlates with spatial memory capability.</li> </ul> |
| <p><b>7.3 Animals learn associations between stimuli and responses</b></p>                     | <ul style="list-style-type: none"> <li>• Learning via Pavlovian conditioning can increase reproductive success in quail and facilitates learning about predators in fish.</li> <li>• Macaques and bees learn new behaviors via operant conditions in a trial-and-error process.</li> </ul>  |
| <p><b>7.4 Social interactions facilitate learning</b></p>                                      | <ul style="list-style-type: none"> <li>• Prairie dogs learn antipredator behavior from adults.</li> <li>• Fish learn food patch quality by observing other conspecifics.</li> <li>• Ptarmigan hens facilitate the chicks learning about food.</li> <li>• Knowledgeable ants facilitate learning by naïve ants about the location of food.</li> </ul>  |
| <p><b>7.5 Social learning can lead to the development of animal traditions and culture</b></p> | <ul style="list-style-type: none"> <li>• Social learning can create different behavioral traditions among populations.</li> <li>• Unique novel food acquisition behavior persisted in different great tit populations through social learning.</li> </ul>   |



## 7.6 Animals vary in their cognitive abilities

- Cognition is the acquisition, storage, retrieval, and use of information for decision making; tool use, insight learning, and numerical competency are often used to assess cognitive abilities.
- Capuchins select the correct stone tools to open palm nuts.
- Elephants and keas exhibit insight learning to acquire food.
- New Zealand robins exhibit numerical competency when retrieving food from caches.
- Brain size and cognitive performance are positively correlated in birds and guppies.
- In bowerbirds, males with high cognitive performance tended to have highest reproductive success.

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- Fiddler crabs learn to habituate to a nonthreatening moving object.

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## CHAPTER 6

# Communication

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 6.1 [Communication occurs when a specialized signal from one individual influences the behavior of another](#)
- 6.2 [The environment influences the evolution of signals](#)
- 6.3 [Signals often accurately indicate signaler phenotype and environmental conditions](#)
- 6.4 [Signals can be inaccurate indicators when the fitness interests of signaler and receiver differ](#)
- 6.5 [Communication can involve extended phenotype signals](#)
- 6.6 [Communication networks affect signaler and receiver behavior](#)

### Features

#### Scientific Process

- 6.1 [Signaling in male wolf spiders](#)
- 6.2 [Fighting fish opercular display](#)

#### Applying the Concepts

- 6.1 [Pheromones and pest control](#)
- 6.2 [Urban sounds affect signal production](#)
- 6.3 [Human luxury brands as costly signals](#)

#### Quantitative Reasoning

- 6.1 [Sand hoods as extended phenotype signals](#)

If you live in the eastern United States near a moist habitat, you may be treated to a remarkable sight. Just after dark each summer evening, many backyards come alive, as fireflies (or lightning bugs) flash on and off. Fireflies are beetles in the order Coleoptera and are bioluminescent—that is, they produce light. If you watch carefully, you can observe differences in the duration and rate of flashes among individuals. You are in fact watching different

species, each with its own distinctive flash pattern for courting conspecifics. The flying males of each *Photinus* species display a species-specific flash pattern to females sitting on vegetation, who respond with their own distinctive flash pattern. Males will land nearby, while continuing to flash, and then mate. The field also contains predatory fireflies in the genus *Photuris*. These species mimic the flashes of *Photinus* females to lure males. Once a *Photinus* male lands nearby, the predatory *Photuris* attacks and eats it ([Figure 6.1](#)) ([Lloyd 1975](#); [Champion de Crespigny & Hosken 2007](#)).



**FIGURE 6.1.** Firefly deception. Predatory female *Photuris* firefly eating a male *Photinus* firefly.

This amazing display is an example of animal communication. As we see in this chapter, animal communication involves an individual's use of signals to influence the behavior of others. Signals are generally believed to be accurate indicators of conditions: the courtship flash displays of male and female *Photinus*, for example, indicate species and sex ([Figure 6.2](#)). However, signals are not always reliable, as the predatory *Photuris* demonstrates. The evolution and accuracy of signals depend on the benefits and costs of signal production and the fitness interests of those involved. While the simplest communication involves two individuals, third-party eavesdroppers can intercept signals, which can affect the behavior of both eavesdroppers and signalers.





**FIGURE 6.2.** Firefly. Fireflies communicate using a bioluminescent flash display.

#### Video: Firefly communication

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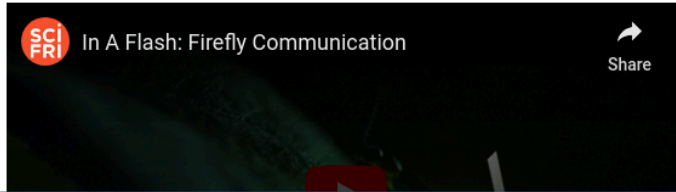
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## 6.1 Communication occurs when a specialized signal from one individual influences the behavior of another

### Learning Objectives

After reading this section, you should be able to

- differentiate between a signal and a cue and
- explain why the honeybee waggle dance and alarm calls are signals.

**Communication** is an interaction in which one individual, a signaler, produces a signal that affects the behavior of another, a receiver. An animal **signal** is an evolved trait that is selected for its effect on the behavior of a receiver and is adaptive for the signaler and, typically, the receiver (Bro-Jorgensen 2010). Signals can take many forms, including the patterns of firefly flashes, chemical pheromones ([Applying the Concepts 6.1](#)), morphological traits like body colors or structures (e.g., horns and antlers), electrical discharges, substrate-borne vibrations, and behaviors such as mating displays and vocalizations. Note that some of these, like vocalizations and behaviors, can be rapidly turned on and off, while others, like morphological structures or chemicals, can persist for longer durations.

### APPLYING THE CONCEPTS 6.1

#### Pheromones and pest control

Up to one-third of the food produced annually worldwide is destroyed by insect pests ([Witzgall, Kirsch, & Cork 2010](#)). One response to this problem has been the widespread use of chemical insecticides. However, these chemicals are not species specific, and many kill nontarget species as well. Insecticides can also facilitate the evolution of resistance by the same pests they are meant to kill ([Witzgall, Kirsch, & Cork 2010](#)). Increasing attention to this issue has produced an alternative solution: the development and use of pheromones as a tool in pest management. Many insects use volatile sex pheromone signals to find a mate. Pheromones can be effective in minute amounts, are species specific, and are environmentally benign. One technique is to release female pheromones throughout a field or orchard, which renders males unable to locate females and thus disrupts mating.

Jianhuamo Mo and colleagues studied the effectiveness of pheromones in controlling damage by light-brown apple moths (*Epiphyas postvittana*) in citrus orchards ([Mo et al. 2006](#)). They compared two orange groves: one control and one into which they released small quantities of an apple moth female sex pheromone. Each orchard contained dozens of individual constrained test females. After one week, females were examined to determine whether they had been inseminated. The researchers found that females in the treatment orchard were almost never inseminated, compared to approximately 50% of those in the control orchard. In addition, examination of orchard fruits revealed that 20% of control orchard fruits had evidence of insect damage, whereas less than 10% of the treatment orchard fruits were damaged. Results like these are encouraging the development of pheromone-based management for various insect pests. ■

Because signals are evolved traits, they differ from cues, which are consistent aspects of the environment that can guide behavior in a way that enhances fitness. For example, a group of vultures on the ground can provide a cue to other scavengers, such as hyenas, about the location of a carcass. Similarly, elevated concentrations of carbon dioxide provide a cue to mosquitoes searching for a vertebrate blood meal. But selection has not acted on the vulture group to communicate the location of a carcass to competitors, nor has it acted on mosquito victims to communicate their location to blood-seeking insects.

Much research on communication has identified different signals and their effect on the behavior of receivers. We begin by focusing on two detailed examples of different types of signals: a behavioral signal in honeybees and a vocal signal commonly observed in mammals and birds.

### Honeybees and the waggle dance

Karl von Frisch was awarded the Nobel Prize in 1973, largely for his work on communication in honeybees (*Apis mellifera*). Honeybees live in colonies, and individual workers leave the hive in search of food. Like many other insects, honeybees use their visual and chemosensory systems to find nectar and pollen. When an individual scout

finds a rich food source, it flies back to the hive and recruits others to help exploit the food. Such communication allows the colony to rapidly exploit the food resource before competitors do. What signal is used to recruit others? In a series of studies, von Frisch manipulated the location of a distant food source and observed the behavior of both scouts and new recruits. He determined that the scout performs a specific behavioral signal that he called the waggle dance ([von Frisch 1967](#)).

### Video: The waggle dance in bees

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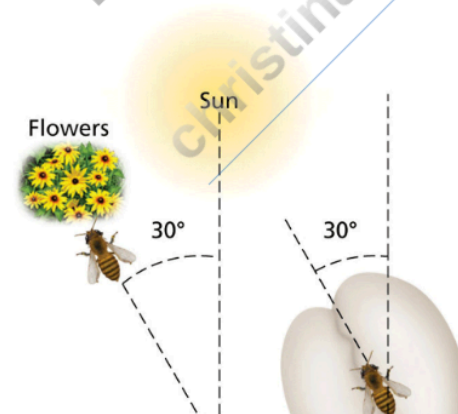
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Video: The waggle dance in bees

indicates the distance to the food. Subsequent work indicates that every 75 milliseconds of wagging translates into a distance of approximately 100 m from the hive ([Figure 6.3](#)) ([Seeley 1985](#)). The waggle dance also describes the direction of the food source, relative to an imaginary line that runs from the hive to the sun. For instance, if the sun is on the horizon (as at dawn) and the scout's linear movement is  $30^\circ$  left of vertical, the food is  $30^\circ$  left of the sun ([Figure 6.4](#)).



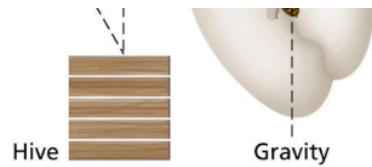
**FIGURE 6.3.** Waggle dance. The waggle dance conveys the direction of and distance to a food source to attending bees. (Source: [Grütter & Farina 2009](#))



During a **waggle dance**, the scout moves in a figure-eight pattern on a vertical wall of the honeycomb. In the linear movement of the dance, the scout vigorously wags its body; the duration of the wagging, von Frisch argued,

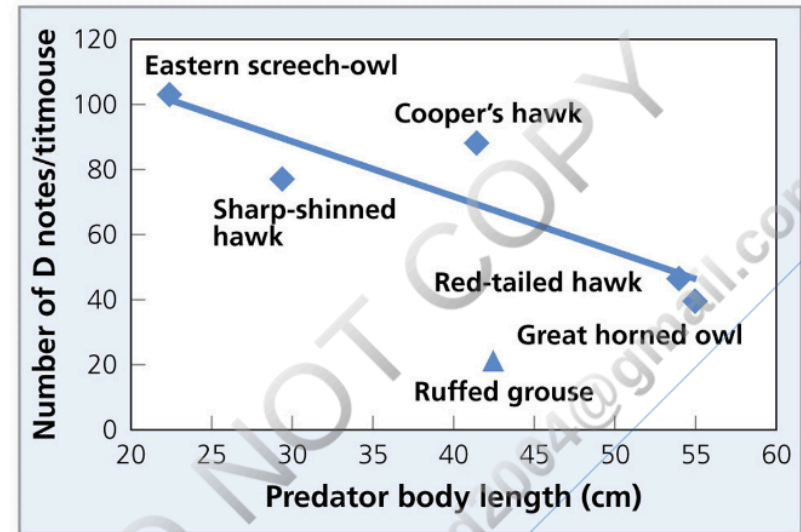
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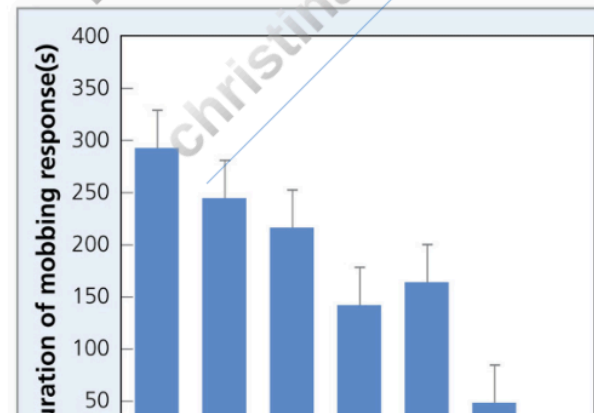


**FIGURE 6.4.** Linear movement of the waggle dance. The bees' linear movement in the vertical plane of the hive (right) indicates the direction of the food relative to the location of the sun (left).

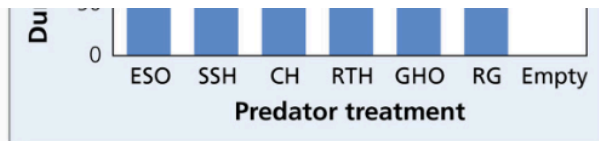
(Figure 6.11): mobbing behavior lasted for approximately 250 seconds for the small-bodied, high-risk predators, compared to only 150 seconds for the larger, low-risk predators and less than 50 seconds for the controls. These results indicate that titmice produce different alarm call signals that correlate with varying levels of threat and lead to differences in the behavior of receivers. This finding illustrates the rapid speed and flexibility of auditory signals in response to changes in the environment.



**FIGURE 6.10.** Alarm calls vary with predator size. Titmice produced more D notes per minute when presented with models of a small predator compared to larger predators or controls. (Source: [Courter & Ritchison 2010](#))







**FIGURE 6.11. Duration of titmouse mobbing behavior.** Mean (+ SE) duration of mobbing behavior for each treatment. Titmice spent more time mobbing models of small predators than they did mobbing larger ones or controls. ESO = Eastern screech-owl; SSH = sharp-shinned hawk; CH = Cooper's hawk; RTH = red-tailed hawk; GHO = great horned owl; RG = ruffed grouse. (Source: [Courter & Ritchison 2010](#))

## Information or influence?

There is an important caveat here. In these and other examples, we do not know whether the signal actually encodes information about conditions, like the presence of a specific predator, although this metaphor has previously dominated work in animal communication (e.g., [Otte 1974](#)). For example, vervet alarm call signals may not mean "leopard present" or "snake present," but rather "climb a tree" or "look down" ([Scott-Phillips 2008](#); [Owen, Rendell, & Ryan 2010](#)). Drew Rendall, Michael Owen, and Mike Ryan contend that the assumption that signals encode specific information is problematic for two reasons ([Rendell, Owen, & Ryan 2009](#); [Owen, Rendell, & Ryan 2010](#)). First, it can imply a language-like meaning of communication that is challenging to document. Second, it can encourage attempts to characterize the information encoded in a signal, rather than focusing on factors that shape signal properties.

Others argue that removing the concept of information from the study of communication is unwarranted ([Carazo & Font 2010](#); [Seyfarth & Cheney 2017](#)), and this discussion continues to stimulate further work. What we can say is that signals influence behavior *as if* they contained information about the location of a food source, the threat of a predator, or the phenotype of a signaler.

Signals vary widely in their physical properties. Next we examine how these differences and the environments through which they travel affect their evolution.

## 6.2 The environment influences the evolution of signals

### Learning Objectives

After reading this section, you should be able to

- describe how an environment could affect different types of signals,
- describe how changes in temperature affect chemical pheromones and the foraging behavior of ants, and

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- compare how the environment influences visual signal transmission in fish and auditory signal transmission in birds.

For effective communication, a signal must travel through the environment from one individual to another, sometimes over long distances. Selection should favor signals that travel most readily through a particular environment, with the least degradation, and that are easy to detect by a receiver ([Endler 1992](#)). Because chemical, morphological (visual), and mechanical (auditory and tactile) signals differ in their physical properties and in how they are produced, they also differ in many other aspects, such as how rapidly they move through the environment, how quickly they can be modified by the signaler, their persistence once produced, and whether they can be blocked by physical objects such as vegetation or rocks.

Chemical signals can be transmitted readily through water or air (when they are **volatile**), are relatively long lasting, and can travel great distances. They can also be deposited on a substrate, as illustrated by the territorial scent marking of mammals ([Figure 6.12](#)) and the foraging trails of ants. Individuals can control the strength of these signals by controlling the amount deposited. In addition, chemical signals can travel around environmental barriers such as dense vegetation. Once transmitted, however, chemical signals cannot be modified, and their effectiveness is greatly impacted by conditions (e.g., temperature, wind, rain).



**FIGURE 6.12. Scent marking.** A wolf marks his territory with urine.

Visual signals, like behavioral displays, move rapidly through the environment and so can be detected quickly,

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allowing a more rapid response. In clear daylight or clear water, they can also be perceived over fairly large distances. However, their perception requires sufficient ambient light levels, and they can be blocked by obstacles. Thus, in deep ocean or murky water and at night, visual signals are ineffective and also do not transmit well in dense vegetation.

Auditory signals are mechanical waves that can bypass obstacles; sound waves can travel around solid objects. That means that auditory signals can sometimes be perceived when visual signals cannot. In addition, auditory signals can be modified rapidly by a sender: they can be turned “on” or “off” depending on conditions (say, when a predator is nearby), and can be produced at different amplitudes (decibel level) to overcome background noise. However, auditory signals can attenuate rapidly (lose energy) as they move through an environment, limiting their effective range. In addition, auditory signals are broadcast widely and so can be detected by many individuals, including predators.

Let's examine three studies that have focused on how environmental conditions have affected the evolution and use of chemical, visual, and auditory signals.

## FEATURED RESEARCH Temperature affects ant chemical signals

Ants live in colonies where offspring are reared. Scouts travel away from the colony to find and retrieve food resources for nest mates. Across species, we see variation in diurnal foraging activity patterns: some species are active all day while others restrict activity when temperatures rise. Variation also exists in foraging strategies. In some species, individual workers search for and bring back food items. In other species, foraging is done socially: a scout that finds a rich food source deposits a volatile chemical pheromone on the surface as it returns to the colony, making a pheromone trail (Figure 6.13). Such signals can persist for 30 or more minutes and allow new recruits to travel directly to the food source. After finding food, new recruits also deposit chemical pheromones as they return to the colony, which maintains the trail until the food is depleted.



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**FIGURE 6.13.** Ant pheromone trail. Recruits follow a pheromone trail to food.

### Video: Ant pheromone trail deposition

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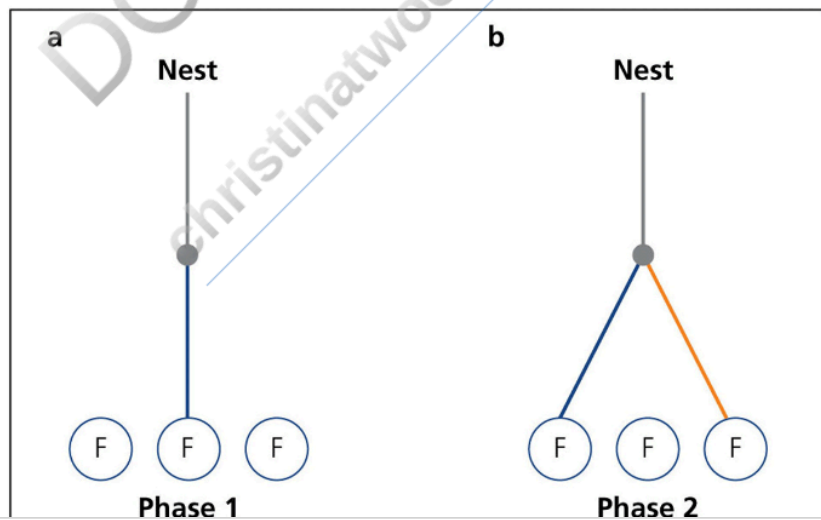
Chemical pheromones in ant food trails are volatile. Therefore, the temperature of the surface should affect the trail. Printed by: christinatwood2004@gmail.com. Printing is for personal, private use only. No part of this book may be reproduced or transmitted without publisher's prior permission. Violators will be prosecuted.



Chemical pheromones in ant food trails are volatile. Therefore, the temperature of the surface should affect the duration of the signal, which should disappear more rapidly in warmer conditions as a result of evaporation. Louise van Oudenhove and her colleagues tested the hypothesis that the persistence of a chemical food trail signal will be negatively affected by surface temperature, which can then affect daily activity patterns. They studied the foraging behavior of *Tapinoma nigerrimum*, a social foraging ant species found throughout the Mediterranean region (van Oudenhove et al. 2011). This species feeds on nectar, and workers deposit volatile chemical trails between a food source and the nest.

The research team first quantified the activity of free-living colonies by counting the number of workers on feeding trails (measured as the number of individuals that crossed a fixed mark over three minutes) once each hour over the course of several days. They simultaneously recorded the surface temperature at the colony entrance. Worker activity was highest for surface temperatures between 20° and 30°C. Activity declined sharply for surface temperatures above 30°C, and there was no worker activity for surface temperatures above 48°C. Clearly, ambient temperature affected foraging behavior in a manner consistent with the hypothesis, but why?

To determine the effect of temperature on pheromone persistence, the research team trained laboratory-housed colonies to feed on a solution of honey and water. Workers were required to cross two sections of a glass bridge to travel from the nest to the food. In the initial phase of the experiment, the colony was allowed to exploit the food patch to establish a pheromone trail across both sections of the bridge. In Phase 2, the second section of the bridge was removed for several minutes and heated to a fixed temperature (25, 30, 35, 40, 50, or 60°C) for ten minutes and then allowed to cool to room temperature (25°C) (Figure 6.14). Simultaneously, a novel section of bridge underwent the same heating and cooling procedure. Once both sections were cool, they were placed at the end of the fixed bridge section in a new Y-shaped orientation. Food was placed at the end of each bridge section, and ants were allowed to travel on either the original or novel section to move to a food patch. The researchers recorded the number of ants using each bridge for ten minutes. If the pheromone persisted after the heating treatment, ants would be expected to preferentially use the original bridge.

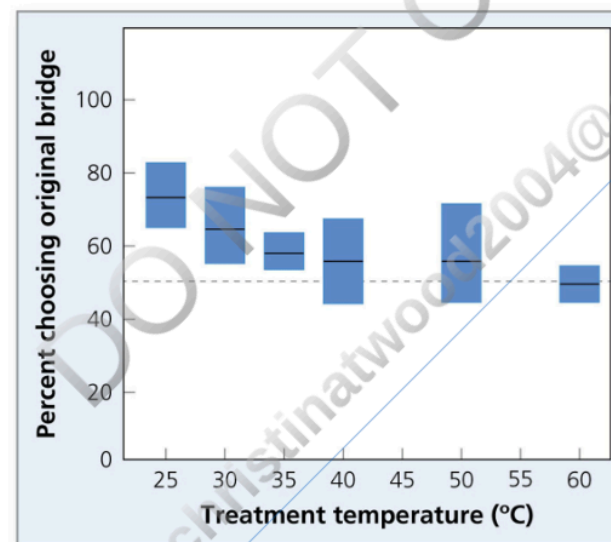


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**FIGURE 6.14. Ant food trail experimental design.** (a) In Phase 1, ants deposited pheromones between the food (labeled F) and the nest on the original bridge (gray and blue). (b) In Phase 2, ants could select either the original bridge (blue) or a new bridge (orange) to move toward a new food location (labeled F) after both bridges had been warmed and then cooled to room temperature.

For the three low-temperature treatments (<40°C), workers preferentially used the original bridge. However, for the three high-temperature treatments (40, 50, and 60°C), there was no significant difference in bridge use (Figure 6.15). These results suggest that surface temperature plays a critical role in food trail persistence and use. At high surface temperatures, chemical pheromone signals are an ineffective communication mode. This may explain why the daily foraging activity patterns of ants that use chemical food trails are restricted to lower surface temperatures. Ambient temperature clearly influences the effectiveness of these chemical pheromones. In a similar manner, visual signals are affected by light level and the visual background environment, as we see next.



**FIGURE 6.15. Experimental bridge choice.** Median percent of workers crossing the original bridge. Each box represents the middle 50% of the data for each treatment temperature. The median is the horizontal line within each box. The dashed line represents 50%. (Source: van Oudenhove et al. 2011)

## FEATURED RESEARCH Habitat light environment affects fish visual signals

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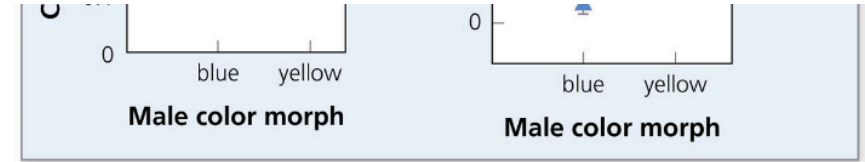
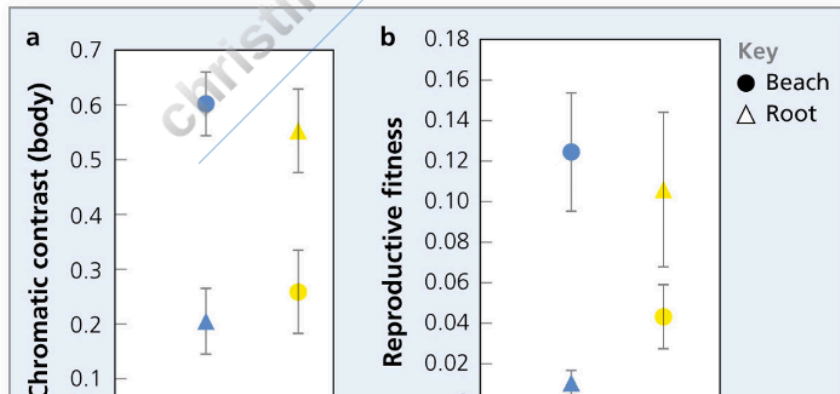


Visual signals often must be detected against a potentially complex visual environment. For effective communication, selection may often favor visual signals that contrast most strongly with the background environment because they can more readily be detected by receivers (Endler 1992; Marchetti 1993). Environments can differ dramatically in both their light level and their spectral properties (dominant wavelengths): consider the difference in light level between a dense forest and an open desert. Environmental light level and spectral properties can also differ dramatically in the same habitat, as occurs in shady and sunny locations within a stream or around a lake.

Suzanne Gray and her colleagues examined the effect of different light environments on the effectiveness of the visual signal in male *Telmatherina sarasinorum*, a small fish found in Lake Matano, Indonesia (Gray et al. 2008). Males exhibit a discrete color polymorphism: they can be either all blue or all yellow. Females are cryptically colored (gray), and so male body color is likely a signal used in communication with females during courtship. Males court females in two distinct habitats: shallow beach sites composed of sand and cobble, and deep-water sites that contain algae-covered roots. These “beach” and “root” sites are interspersed, and all males and females visit both habitats to reproduce.

To humans, these habitats appear to present different light levels and visual backgrounds. Gray and her colleagues wondered whether females preferentially mate with males based on the effectiveness of their color display in each habitat. In particular, they tested the prediction that a male’s reproductive success will be highest in habitats in which his body color contrasts most strongly with the visual background, because in such conditions his visual signal should be most effective.

The researchers established 12 transect sites (six in each habitat). They first captured males along each transect and used a radiometer to measure (1) the color spectrum (wavelengths of visible light) reflected from the sides of the fish’s body and (2) the associated habitat background color spectrum under ambient light levels. The level of chromatic contrast between a male and his environment was calculated using spectral sensitivities of fish retinal photopigments to quantify a fish’s perception of the contrast (Chapter 5). Analyses of the spectral properties of each morph in each habitat revealed that the blue morph contrasted most strongly with the beach habitat color spectrum, while the yellow morph contrasted most strongly with the root habitat color spectrum (Figure 6.16). Does male morph color affect reproductive success differently in each habitat, as predicted?



**FIGURE 6.16. Chromatic contrast and reproductive fitness.** (a) Mean ( $\pm$  SE) chromatic contrast. Blue males had high chromatic contrast in the beach habitat (circles), while yellow males had high contrast in the root habitat (triangles). (b) Mean ( $\pm$  SE) reproductive fitness. Blue males had the highest fitness in the beach habitat (circles), while yellow males had the highest fitness in the root habitat (triangles). (Source: Gray et al. 2008)

To answer this question, the research team needed to characterize the reproductive success of males of each morph in each habitat. In this species, two male mating tactics exist. Some males perform active mating displays to attract females, while other males do not display and are known as “sneakers.” Females sometimes mate with one displaying male that fertilizes all her eggs. However, if one or more sneaker males are present at the mating, they can fertilize eggs by releasing sperm near the spawning site of the pair. In this case, all males that release sperm fertilize eggs. Both male morphs use both strategies in both habitats studied.

To quantify the reproductive success of males in each habitat, observers conducted focal observations of individual males and females for up to ten minutes, recording all spawning events, the presence of all sneaker males, and the color morph of each male present during a spawning event. To quantify the reproductive success of each male morph in each habitat, the researchers assumed that eggs were fertilized equally by all males present (e.g., when only one male was present, he fertilized 100% of the eggs; when two males were present, each fertilized 50% of the eggs, and so forth). These data allowed the research team to characterize the mating success of both male morphs in each habitat.

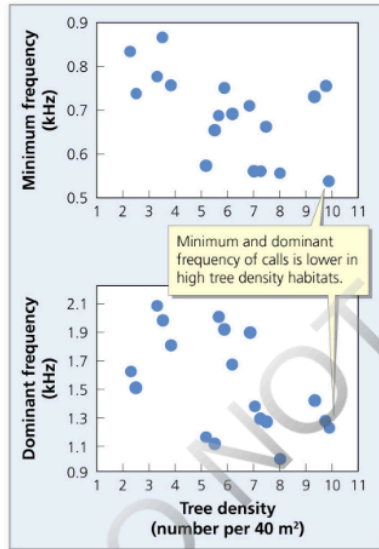
As predicted, each male morph had its highest reproductive success in the habitat in which its morphology contrasted most strongly with the background environment: blue morphs had higher reproductive success in the beach habitat, while yellow morphs had higher reproductive success in the root habitat (Figure 6.16). These data support the prediction that visual signal effectiveness is affected by background environmental properties and may help to explain the evolution of different male coloration signals in this species.

Finally, let’s consider how the environment affects auditory signals.

## FEATURED RESEARCH Habitat structure affects bowerbird auditory signals

To be effective, auditory signals must be detected over background noise: they must stand out from their environment. Auditory signals can travel over long distances, but they degrade (lose quality) and attenuate (lose intensity) as they travel; furthermore, the rates of degradation and attenuation are affected by habitat structure. For example, higher frequencies attenuate more rapidly in dense vegetation (Blumenrath & Dabelsteen 2004), which should favor the use of lower frequencies, because selection should favor individuals whose

As predicted, call structure varied across sites and was related to habitat type. Minimum frequency and dominant frequency were negatively correlated with tree density—that is, they were lower in sites with more trees ([Figure 6.18](#)). What produces these population differences? One possibility was that morphological differences across populations, such as body size, could account for this correlation, but after examining the data, the researchers ruled this explanation out. Another possibility concerns learning: juveniles may simply learn those habitat-specific calls that they hear best. Further work is required to test this hypothesis.



**FIGURE 6.18. Bowerbird call variation and habitat structure.** The minimum and dominant frequencies of calls are lower in habitats with higher tree density. Each point represents the mean values for each location. (Source: [Nicholls & Goldizen 2006](#))

These examples show how the environment can affect signal use and evolution. Recall that the function of communication is to influence the behavior of another individual. As such, the evolution of signals is strongly influenced by the fitness interests of both signaler and receiver. This aspect is the focus of the rest of the chapter.

## 6.3 Signals often accurately indicate signaler phenotype and environmental conditions

### Learning Objectives

After reading this section, you should be able to

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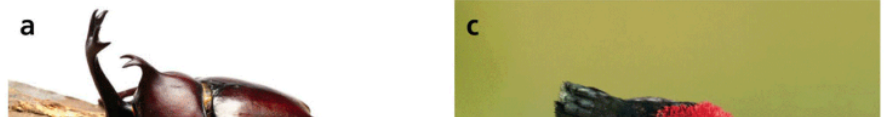
- identify the three conditions that favor the evolution of signals as accurate indicators of conditions,
- explain why aposematic coloration is an honest signal, and
- provide one example in which a behavior was an honest signal.

For signals to evolve, they must increase the fitness of the signaler. Because signals affect the behavior of another individual, selection on signals will also be affected by receivers. Receiver behavior should not be influenced by signals that do not enhance their own fitness. As a result, the fitness interests of signalers and receivers may differ, which will affect the evolution of a signal. In particular, the potentially divergent interests can lead to two outcomes. In the first, the signal will evolve to become an accurate indicator of signaler phenotype or the environment. In the second, the signal will evolve to become an inaccurate indicator of conditions. We start by examining the former outcome and then address the latter in the next section.

### Signals as accurate indicators: theory

Three conditions favor the evolution of signals as accurate, or “honest,” indicators ([Maynard Smith & Harper 2003](#)). First, if the fitness interests of the signaler and the receiver are similar, both parties will benefit from an accurate relationship between the signal and the signaler phenotype or environmental conditions. Second, we can expect signals to be accurate indicators when they cannot be faked. Suppose, for example, that a signal is a function of body size. In contests over resources or territories, males often produce vocal signals. The frequency of a vocalization, or its pitch, is often negatively related to body size. For example, only the largest males with the longest sound-producing structure—such as the larynx in frogs and mammals or the harp in crickets—can produce the lowest-frequency vocalizations ([Clutton-Brock & Albon 1979](#); [Scheuber, Jacot, & Brinkof 2003](#)). In these cases, the ability to produce low-frequency vocalizations is an accurate signal indicator of male size.

Finally, and perhaps most commonly, signals may be accurate indicators because they are costly to produce or maintain ([Zahavi 1975](#); [Grafen 1990](#)). For example, the long horns of beetles used in aggressive interactions ([Emlen 1994](#)), the wide eye span of stalk-eyed flies ([David et al. 2000](#)), and the wattle size and color of pheasants used to attract mates ([Ohlsson et al. 2002](#)) are physiologically costly to produce: only males with access to abundant resources possess the largest, most extreme form of these traits ([Figure 6.19](#)). Other signals used in courtship include behavioral displays and the bright plumage or body coloration of many birds and fish, which are also costly to produce and maintain: they make the male more visible ([Magnhagen 1991](#)) and are therefore found in those individuals best able to avoid predators. Because they are accurate indicators of male phenotype, females frequently prefer mates with extreme signals (see [Chapter 12](#)).



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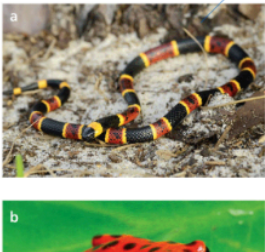


**FIGURE 6.19. Costly traits.** (a) Horn length in beetles, (b) eye span in stalk-eyed flies, and (c) wattle size and red color in pheasants are examples of traits that are costly to produce: each is larger and/or more intense when individuals have access to better diets.

Many signals are considered to be accurate indicators because one of these three conditions exists. Next, we illustrate examples of accurate signals with studies of predation, courtship, and aggression. In the first, the fitness interests of predator and prey are similar. The latter two illustrate how the high fitness cost of a behavioral signal can lead to accurate indicators of signaler phenotype.

## FEATURED RESEARCH Aposematic coloration in frogs

Some species possess **aposematic coloration**—bright coloring on their bodies that makes them stand out from the environment and indicates that they contain noxious chemicals or poisons that make them unpalatable or dangerous prey. Such coloration is common in insects but is also found in fishes, amphibians, and snakes (Figure 6.20) (Ruxton, Sherratt, & Speed 2005). These species benefit if predators learn to avoid attacking them. Predators, too, benefit by learning such an association, because they will then not waste time hunting unpalatable prey.



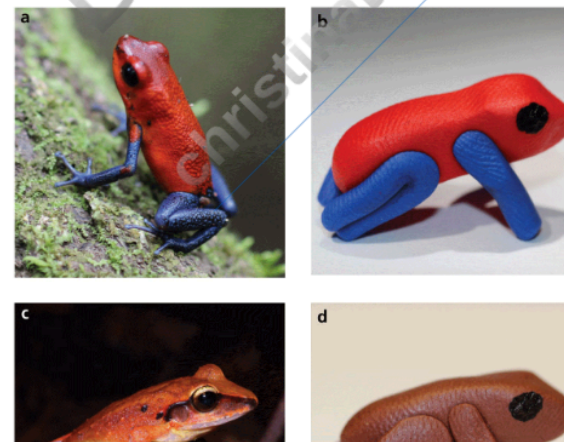
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**FIGURE 6.20. Aposematic coloration.** (a) Coral snake, (b) poison dart frog, and (c) cinnabar moth caterpillar. All of these species are unpalatable to predators.

Ralph Saporito and colleagues conducted an experiment to investigate whether the bright body coloration in the dendrobatid frog (*Oophaga pumilio*) functions as an aposematic signal. This frog commonly lives in leaf litter in the tropics and has a bright reddish-orange dorsal color with blue appendages. Dendrobatid frogs contain skin alkaloids that predators find distasteful (Daly & Myers 1967; Daly, Spande, & Garraffo 2005).

Saporito's team examined predation attempts on clay models molded to resemble the toxic *O. pumilio* and a nontoxic, brown leaf-litter frog similar to frogs of the genus *Craugastor* (Figure 6.21) (Saporito et al. 2007). Each model measured approximately 20 mm in length, the average size of *O. pumilio* in the study region in Costa Rica. To quantify predation, the researchers placed 800 frog models on either the forest floor or a white piece of paper at 5 m intervals along 40 transects. The white paper was used to take into account the effect of cryptic coloration, since half the brown models would then be obvious to predators. After 48 hours, the models were collected. The soft modeling clay retained impressions from predation attempts. Birds left U- or V-shaped attack marks, while mammals left teeth marks.



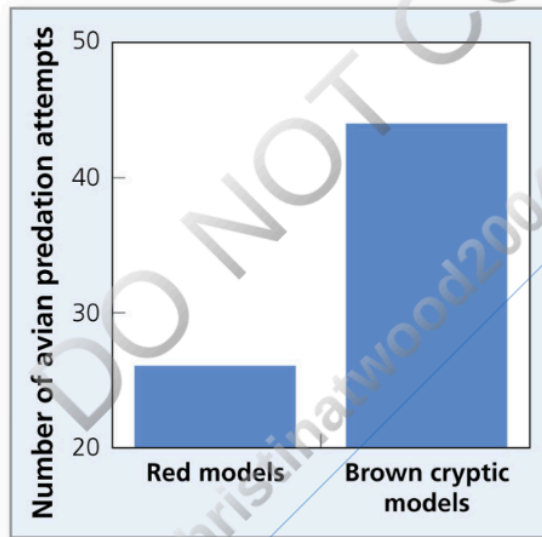
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**FIGURE 6.21. Clay models and frogs.** (a) Toxic *Oophaga pumilio* and (b) its clay model. (c) Nontoxic *Craugastor fitzingeri* and (d) its clay model.

Over 12% of the models were attacked, mostly by birds. Although more models placed on the forest floor were attacked than those placed on white paper, the difference was not significant. However, the brown models were attacked by birds at almost twice the rate of the brightly colored models (Figure 6.22). These data support the hypothesis that bright coloration is a signal to predators that prey are unpalatable. Bright body coloration benefits the signaler when predators associate the colors with distasteful prey, allowing them to learn to avoid such items.



**FIGURE 6.22. Predator attacks on frog models.** Brown cryptic models were attacked more often than red (aposematic) models. (Source: Saporito et al. 2007)

## FEATURED RESEARCH Courtship signaling in spiders

Chad Hoefer and colleagues studied the mating behavior of wolf spiders (*Pardosa milvina*) to determine if males display accurate signals of their quality to females (Hoefer, Persons, & Rypstra 2008; Hoefer et al. 2009). In the presence of a female (or silk containing female pheromones), males engage in active displays that involve leg

raises. Females prefer to mate with those males that display the most intense courtship behaviors (Rypstra et al. 2003). Hoefer and his research team hypothesized that male condition affects leg raising rate and so predicted that males in good condition should perform leg raises at a higher rate than those in poor condition (Scientific Process 6.1).

### SCIENTIFIC PROCESS 6.1

#### Signaling in male wolf spiders



Research Question: Do male wolf spider leg raises provide an accurate signal to females?

#### Hypothesis (1):

Male condition affects leg-raising rate.

#### Prediction (1):

Good-condition males will display at a higher rate than poor-condition males.

#### Hypothesis (2):

High display rate in males indicates high quality.

## Prediction (2):

Females mated to males with high leg display rates will have higher reproductive success.

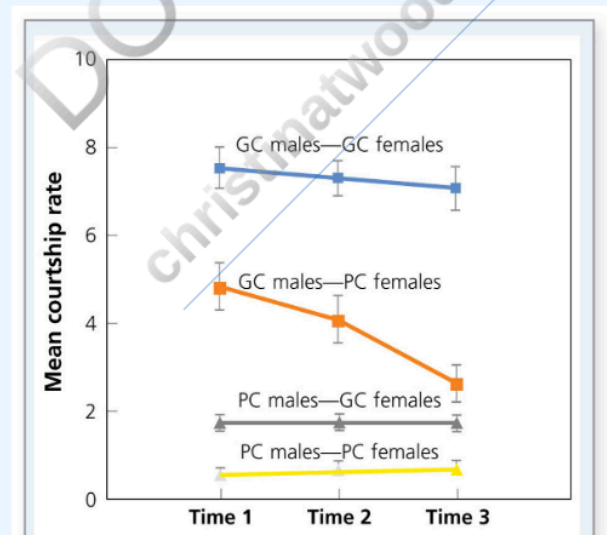
## Methods (1):

The researchers:

- Collected 60 juvenile male and 60 juvenile female spiders and raised them in the lab for three weeks. Poor-condition treatment (PC) spiders were fed one cricket twice per week. Good-condition treatment (GC) spiders were fed four crickets twice per week.
- Created four mate-pairing test groups:
  - GC male with GC female
  - GC male with PC female
  - PC male with GC female
  - PC male with PC female
- Measured male courtship rate in a cylindrical arena (8 cm high × 19 cm diameter)
- Repeated the trial for the next three days using the same individuals to test for consistency

## Results (1):

GC males displayed at higher rates than PC males. Display rate was consistent across times, except for GC males mated to PC females.



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**FIGURE 1. Courtship.** Mean ( $\pm$  SE) courtship rate over trials for each treatment. (Source: [Hoeffer et al. 2009](#))

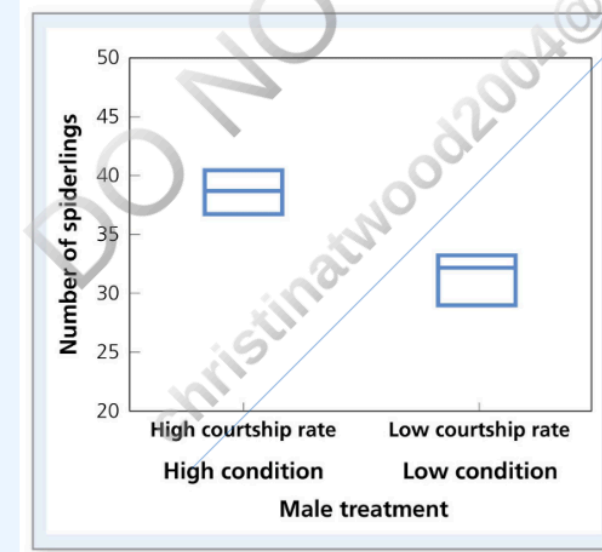
## Methods (2):

The researchers:

- Mated females with males in two groups:
  - Males ( $n = 21$ ) with high leg display rates (5.9 leg raises/min)
  - Males ( $n = 36$ ) with low leg display rates (3.0 leg raises/min)
- Measured the number of spiderlings and their survival

## Results (2):

Females mated to males with a high display rate had more spiderlings and higher offspring survival than females mated to males with a low display rate.



**FIGURE 2. Reproductive success.** Reproductive success of females mated to males with different courtship rates. Each box represents the middle 50% of the data. The median is each horizontal line. (Source: [Hoeffer et al. 2009](#))

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### Conclusion:

Mate condition affects male courtship display rate and is an accurate signal of male quality and fitness.

### Evaluate

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What fitness benefit do females obtain by mating with males that exhibit high display rates?

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They tested this prediction by conducting two experiments that manipulated the condition of males and females and tested their behavior over three days. As predicted, a male's condition affected his behavior. Males in good condition displayed leg raises at higher rates than males in poor condition. In addition, male behavior was consistent over all three days in three of the four test groups. Females that mated with males with high display rates had higher fitness: they had more spiderlings than females that mated with males with low display rates, and

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rates had higher fitness. They had more spiderlings than females that mated with males with low display rates, and their spiderlings lived significantly longer. Taken together, these results indicate that male display is an accurate signal of male quality: only males in good condition were able to maintain a high display rate, and display rate was generally consistent over time. Females obtained fitness benefits by mating with males that displayed at high rates.

One interesting observation was that good condition males, when matched with females in poor condition, exhibited declining display rates over the three days. How can we interpret this behavior? All males that displayed to a female whose condition was similar to or higher than their own displayed highly repeatable courtship levels over each day, indicating that males are capable of continuing with the high rate of leg raises. Perhaps it was not beneficial for males that perceived a female to be in poor condition to expend the energy to continue a high-intensity courtship. This hypothesis remains to be tested.

## FEATURED RESEARCH Aggressive display and male condition in fighting fish

Accurate signaling is also common in a third context: aggressive interactions. Many animals, including fish, engage in aggressive contests over food and mates (see [Chapter 11](#)). When two fish fight, they often begin by engaging in a head-on opercular flare—an encounter in which the opercula, the bony flaps that cover the gills, flare out at the opponent. The frequency and duration of the display increase during a contest, and both are strongly correlated with winning: individuals that have high flare rates and long flare durations typically win.

Mark Abrahams, Tonia Robb, and James Hare hypothesized that the opercular flare display is an accurate signal of fighting condition because it is costly ([Abrahams, Robb, & Hare 2005](#)). The opercula play an important role in respiration. For the gills to function properly in gas exchange, they must be adequately ventilated by moving water. In calm water, ventilation is accomplished through opercular movements. Fish engaged in long flare displays in calm water must therefore sacrifice normal flapping movement and consequently water ventilation. Abrahams and colleagues hypothesized that only individuals in the best physiological condition would be able to sustain long opercular displays because of this cost. To test this hypothesis, they measured the ability of fish to maintain long opercular displays in normoxic (normal oxygen level) and hypoxic (low oxygen level) water. They predicted that flare displays would be significantly shorter under hypoxic conditions ([Scientific Process 6.2](#)).

### SCIENTIFIC PROCESS 6.2

#### Fighting fish opercular display



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Research Question: Does opercular display behavior vary with the condition of a fish?

### Hypothesis:

Opercular displays are costly to perform at high rates because they reduce water ventilation over the gills.

### Prediction:

Males in the best physiological condition will perform opercular displays at a higher rate than individuals in poorer condition.

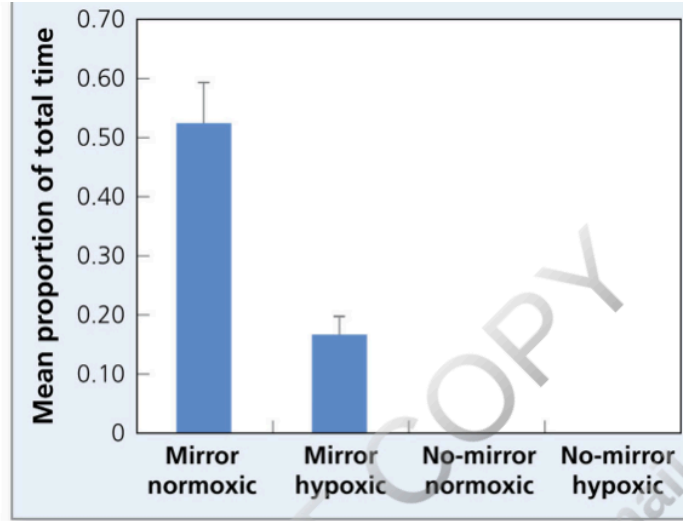
### Methods:

The researchers:

- Manipulated males by placing individuals in water that differed in oxygen level: normoxic water (at least 4 ppm dissolved oxygen) allowed fish to remain nonstressed; hypoxic water (3 ppm dissolved oxygen), created by bubbling nitrogen into the water, produced stressed individuals.
- Recorded fish display behavior in ten-minute trials for two treatments: with or without an intruder (represented by a mirror image in the test tank)
- Recorded the percentage of time a fish spent displaying (operculum flared out) over the course of 19 trials

### Results:

Fish in normoxic water displayed significantly more than fish in hypoxic water.



**FIGURE 1.** Displays. Mean (+ SE) proportion of time displaying across treatments. (Source: [Abrahams, Robb, & Hare 2005](#))

### Conclusion:

Only males in good physiological condition can display at a high rate. Opercular displays are an accurate signal of male condition.

### Evaluate

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What is the assumed relationship between opercular flare rate and fighting

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The team examined the behavior of a popular freshwater species, Siamese fighting fish (*Betta splendens*), known for its aggressive behavior. Fish were exposed to four experimental treatments that varied in both dissolved oxygen level (normal or hypoxic) and the presence or absence of an intruder. To simulate an intruder, the researchers placed a mirror behind a removable opaque partition at one end of the tank. Fish appear to perceive their image in a mirror as an intruder and will display aggressively toward it.

Fish did not display when there was no “intruder” but readily displayed to the “intruder” that appeared in the mirror. In addition, opercular display behavior was significantly lower in hypoxic than normoxic conditions, as predicted. Abrahams and colleagues concluded that opercular displays are accurate signals of physiological condition because they are costly. They suggest that opercular displays cannot be faked: a fish flaring its operculum is analogous to a terrestrial vertebrate holding its breath. Only individuals in good physiological condition can maintain long opercular flare displays.

These examples show how, and under what conditions, signals can be accurate indicators of signaler phenotype or environmental conditions; recent work has even applied these ideas to humans ([Applying the Concepts 6.3](#)). However, not all signals are accurate indicators of phenotypes or conditions, as we see next.

### APPLYING THE CONCEPTS 6.3

#### Human luxury brands as costly signals

Luxury products are priced at a substantial premium, but most provide essentially the same function as nonluxury products (think about brands of clothes, handbags, or watches). Why do consumers purchase these costly items? Are these signals that influence the behavior of others (e.g., [Bouska & Beatty 1978](#))? Can we understand such behavior in the context of animal signaling theory?

Ron Nelissen and Matijn Meijers conducted a set of experiments designed to answer these questions ([Nelissen & Meijers 2011](#)). They hypothesized that because displays of luxury brands

are costly, these signals should be perceived as accurate indicators of status and wealth. Further, the researchers investigated the benefits of producing such a display.

In one experiment, undergraduates viewed one of two videotaped job interviews of a man seeking employment as a laboratory assistant. The two videos differed only in the man's polo shirt logo (either the luxury-brand logo Tommy Hilfiger or no logo). Based on the video, the participants were asked to rate the applicant's suitability for the job, how much he should be paid, his status, his attractiveness, his kindness, and his trustworthiness. When the man was wearing the luxury-brand logo, participants rated him as more suitable for the job, deserving of a higher wage, and of higher status than when he was wearing no logo.

This experiment suggests that luxury-brand labels may act as a signal that affects receiver perception of, and behavior toward, the signaler. Those wearing luxury brands are perceived as being of higher status and wealth and as worthy of higher pay. The result is a benefit for the signaler (e.g., the acquisition of more money). Animal signaling theory can help explain how and why such behavior occurs. ■

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## 6.4 Signals can be inaccurate indicators when the fitness interests of signaler and receiver differ

### Learning Objectives

### Learning Objectives

After reading this section, you should be able to

- identify the conditions that can favor the evolution of inaccurate signals,
- explain why the production of inaccurate signals should be relatively rare in a population, and
- provide one example of an inaccurate signal.

Not all communication involves accurate signals. What happens when the fitness interests of signaler and receiver conflict, as in our predator–prey firefly example at the beginning of this chapter? In such cases, the signaler can benefit by producing an inaccurate, or “dishonest,” signal. But when inaccurate signals exist, receivers that are able to discriminate accurate from inaccurate signals will also benefit. This produces a coevolutionary arms race ([Dawkins & Krebs 1979](#)) between signalers and receivers: signalers are selected to produce signals that affect the behavior of receivers in ways that enhance signaler fitness (e.g., by producing inaccurate signals that are difficult for receivers to discern), and receivers are selected for better discrimination abilities so that they are not influenced by inaccurate signals ([Rice & Holland 1997](#); [Holland & Rice 1998](#); [Lozano 2009](#)). Who wins in such a “race”? Neither. The evolution of the signal trait and its effect on receivers is an ongoing process: it is influenced by the fitness benefits and costs of signal production and accuracy in the signaler and discrimination ability in the receiver ([Krebs & Dawkins 1984](#); [Dawkins & Guilford 1991](#); [Johnstone & Grafen 1993](#); [Rowell, Ellner, & Reeve 2006](#)).

Inaccurate signals are common in interspecific signaling, such as between prey and predators. Here, the fitness interests of the species differ radically: prey fitness is enhanced by avoiding predation, while the predator benefits from consuming the prey. One well-known case of inaccurate signaling is **mimicry**—the adaptive resemblance of one species (the mimic) to another (the model) so that a third species (the receiver) is duped. In **Batesian mimicry** ([Bates 1862](#)), a palatable mimic resembles an unpalatable model that predators have learned to avoid. The predator perceives an inaccurate signal from the mimic and so does not attack it. In this case, the relative fitness benefit of the signaler favors the evolution of a signal that is difficult to discern. A poor signal that is easy to discern will lead to the death of the signaler, but an effective signal will only result in the loss of a meal for the predator. A second example is **aggressive mimicry**, in which a predator mimics a nonthreatening model species in order to gain access to food. Again, the receiver is duped, but in this case, it is attacked by the aggressive mimic (as we saw in the *Photuris* and *Photinus* fireflies). Let’s look at one detailed example of each.

### FEATURED RESEARCH Batesian mimicry and yellow-eyed salamanders

As we saw earlier, aposematism, or bright warning coloration, is commonly found in species with toxins. These visual signals evolved to convey accurate information to predators about the unpalatability of a prey species, and both signaler and receiver benefit from it. However, this signaling system is also ripe for “deceit,” or inaccurate signaling. Individuals of a third species that does not produce a toxin, the Batesian mimic, can benefit if they resemble the toxic model species.



Batesian mimicry is found in many animal taxa. Shawn Kuchta, Alan Krakauer, and Barry Sinervo examined mimicry in *Ensatina* salamanders which live throughout central California (Kuchta, Krakauer, & Sinervo 2008). Most subspecies are cryptically colored, but one, the yellow-eyed salamander (*Ensatina eschscholtzii xanthoptica*), is brightly colored. As its name suggests, it has yellow eyes, and its legs and ventral region are bright orange. Is it a Batesian mimic? One hypothesis is that it mimics aposematic toxic newts in the genus *Taricha* (Figure 6.23) (Stebbins 1949). *Taricha* newts and the yellow-eyed salamander co-occur geographically, and both possess an orange ventral region and bold yellow patches in the iris.



**FIGURE 6.23. Salamander mimicry.** *Ensatina* salamander mimic (right) and its toxic model (left). Note their yellow eye coloration and orange ventral surface.

### Video: Ensatina salamander walking

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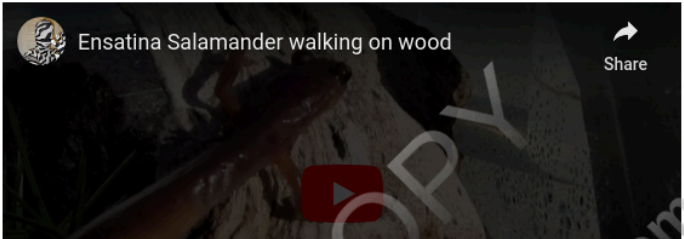
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Video: Ensatina salamander walking



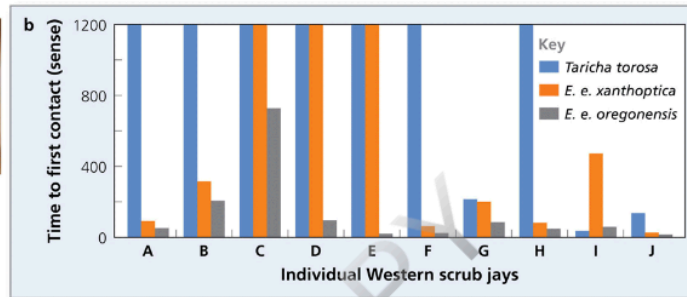
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To test this hypothesis, the research team conducted a series of feeding trials with Western scrub jays (*Aphelocoma californica*). Scrub jays feed on a variety of insects and small terrestrial vertebrates, including salamanders. In the experiment, wild jays were captured and housed individually in a large aviary. On the first day, all jays were presented with an edible salamander (*Batrachoseps attenuatus* or *B. luciae*) to ensure that they would eat salamanders. The next day, they were presented with a toxic newt (*Taricha torosa*). On the third day, each bird was presented with either a yellow-eyed salamander (mimic) or a cryptic palatable subspecies *Ensatina eschscholtzii oregonensis*. On the final day of the experiment, each jay was given the other subspecies of *Ensatina*. All salamander prey were first euthanized to eliminate behavioral differences and thus force jays to make feeding decisions based on morphology alone. Prey were presented in a lifelike posture in the middle of the aviary.

The researchers found that seven of the ten jays did not touch the toxic model. Three jays briefly poked at it but did not attempt to consume it. These ten individuals had apparently learned to avoid the toxic prey in the wild. However, the jays' behavior differed with respect to the two salamander subspecies. All ten birds contacted the cryptic palatable subspecies, *E. e. oregonensis*, more quickly than they contacted the yellow-eyed salamander. The latter were not even touched by three of the jays (Figure 6.24). Yellow-eyed salamanders were consumed in only half the trials, whereas the palatable cryptic subspecies was consumed in nine out of ten trials. The researchers concluded that the yellow-eyed salamander effectively mimics the coloration of the toxic newt *T. torosa*, thereby obtaining a fitness benefit. The mimicry was not perfect: jays consumed more salamander mimics than they did toxic models. Nonetheless, attack intensity on mimics was less than on nonmimics, so we can see how selection would favor the evolution of Batesian mimicry as an inaccurate morphological signal.



**FIGURE 6.24.** Jay attacks on salamander models and mimics. (a) Western scrub jay. (b) Time to first contact with models for ten birds (A–J). Scrub jays rarely contacted the toxic model (blue). Jays took longer to contact the mimic *Ensantina* salamander (orange) than the cryptic salamander (gray). (Source: [Kuchta, Krakauer, & Sinervo 2008](#))

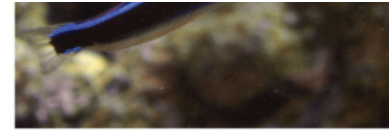
## FEATURED RESEARCH Aggressive mimicry in fangblenny fish

Recall that in aggressive mimicry, a predator mimics a nonthreatening model so that it can closely approach its prey. Karen Cheney and Isabelle Côté examined aggressive mimicry in a coral reef system in Australia ([Cheney & Côté 2007](#)). Ectoparasites, such as gnathiid isopod larvae, infest many reef fish ([Grutter 1994](#)). These ectoparasites are also a food source for **cleaner fish**—small fish that feed on parasites and the dead skin of larger fish. In essence, the cleaner fish performs a service to the parasitized “client” fish, creating a mutualistic relationship. However, when client fish have few parasites, cleaner fish may feed on healthy tissue and can harm clients ([Cheney & Côté 2005](#)), so the mutualism depends on how heavily the client fish is parasitized.

The juvenile bluestreak cleaner wrasse (*Labroides dimidiatus*) is a common cleaner fish found throughout the Indo-Pacific. Another species, the bluestriped fangblenny (*Plagiotremus rhinorhyncos*), closely resembles the bluestreak wrasse but consumes only the healthy scales, mucus, and dermal tissue of client fish. Both species have black bodies with neon blue stripes ([Figure 6.25](#)). Given this close morphological resemblance, Cheney and Côté tested the hypothesis that fangblennies are aggressive mimics of juvenile cleaner fish. Clients with high parasite loads, they predicted, should seek interactions with cleaners and so may not be as vigilant about discriminating a cleaner from a fangblenny. On the other hand, clients with low parasite loads have less to gain by interacting with cleaners and so should be more vigilant to deception.



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**FIGURE 6.25.** Cleaner and mimic. There is a close resemblance between (a) the fangblenny mimic and (b) the bluestreak cleaner model.

Staghorn damselfish (*Amblyglyphidodon curacao*) ([Figure 6.26](#)), a common reef client fish, were collected from a site in the Great Barrier Reef along with juvenile bluestreak cleaner fish and fangblennies. The experiment consisted of a treatment (damselfish parasitized) and a control (damselfish not parasitized). To parasitize damselfish, a fish was confined to a small section of a tank, where approximately ten unfed gnathiid isopods were released. On average, approximately six isopods attached themselves to the fish, a typical parasite load for *A. curacao*. Unparasitized fish were left free of isopods. During each trial, all three fish were allowed to interact for 15 minutes, and the researchers recorded the amount of time damselfish spent being cleaned by the cleaner fish, which fish (cleaner or client) terminated the interaction, the number of times the damselfish avoided an interaction with the cleaner fish, the number of successful attacks by the fangblenny on the damselfish, and whether the damselfish aggressively chased the fangblenny or cleaner fish.



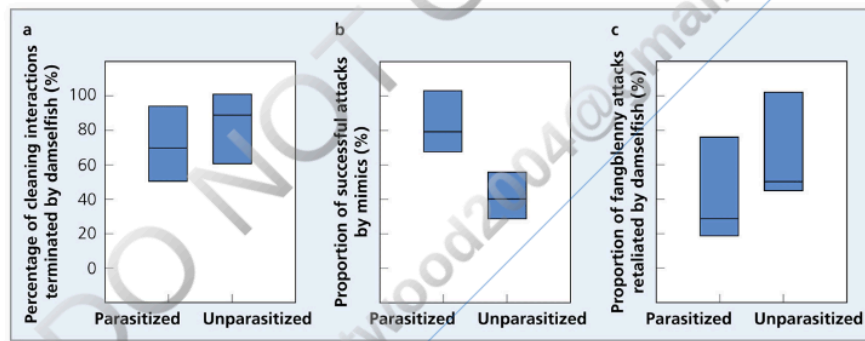
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**FIGURE 6.26.** Staghorn damselfish. A common reef fish in the western Pacific.

Cheney and Côté found that parasitized damselfish were cleaned for a longer period of time than were unparasitized individuals. In addition, parasitized individuals terminated fewer cleaner fish interactions and avoided cleaner fish less than did unparasitized fish (Figure 6.27). These findings indicate that parasitized damselfish benefited from interactions with cleaner fish, just as expected. Fangblennies also attacked parasitized and unparasitized fish at a similar average rate of 4.5 times per 15-minute observation. However, the proportion of successful attacks was higher on parasitized damselfish. In addition, parasitized damselfish retaliated less often to fangblenny attack than did unparasitized fish.



**FIGURE 6.27.** Interaction between damselfish and cleaner fish. Parasitized damselfish (a) terminated fewer interactions with cleaner fish, (b) were attacked more successfully by fangblennies, and (c) initiated fewer retaliatory chases than did unparasitized damselfish. In each plot, the median is represented by the horizontal line, and the box represents the middle 50% of the data. (Source: Cheney & Côté 2007)

These data suggest that fangblennies in this system are aggressive mimics of juvenile cleaner fish, and that their success depends on the state of a client fish. Cheney and Côté suggest that when client fish have higher rates of parasitism, they are more likely to seek out interactions with cleaner fish. Because of the benefits of parasite removal, client fish are willing to incur the costs of mimics and so are less vigilant. This allows aggressive mimics like fangblennies to be more successful.

## Intraspecific deception: false alarm calls

So far, our examples have involved mimicry and interspecific “deception,” or inaccurate signaling between

species. Within-species, or intraspecific, deception also occurs but is less common for two reasons. First, intraspecific interactions are more common, and so individuals can learn to ignore inaccurate signals faster (Dawkins & Guilford 1991; Johnstone & Grafen 1993). We can say that inaccurate signals are subject to negative frequency-dependent selection, which keeps them rare, as we discussed in Chapter 3. Second, recall that natural selection will favor receivers that can discriminate accurate from inaccurate signals. For instance, we have seen that male quality is often associated with a morphological or behavioral signal. Since poor-quality males can benefit by providing an inaccurate signal, how do females avoid deception? Selection will favor females that focus on signals in males that are costly to produce or difficult to fake (Zahavi 1975; Grafen 1990). Inaccurate signals will then yield low fitness, because they will be ignored.

However, one type of signal that involves deception of conspecifics is the production of false alarm calls—alarm calls that are produced when no threat is nearby. Let’s look at two examples. In each case, the caller produces an inexpensive inaccurate signal and then takes advantage of its effect on receiver behavior.

## FEATURED RESEARCH Topi antelope false alarm calls

Topi (*Damaliscus lunatus*) are large antelope (weighing 75–150 kg) that live in the open savannahs of sub-Saharan Africa. When topi spot a predator—such as a lion or even humans—they emit snort vocalizations and then stare in the direction of the predator with their ears pricked up (Figure 6.28). Alarm snorts likely function to inform a predator that it has been spotted, because many predators can successfully capture prey only when they have the element of surprise (see Chapter 9).



**FIGURE 6.28.** Topi. A male with a female in his territory gives an alarm snort and looks off to the distance.

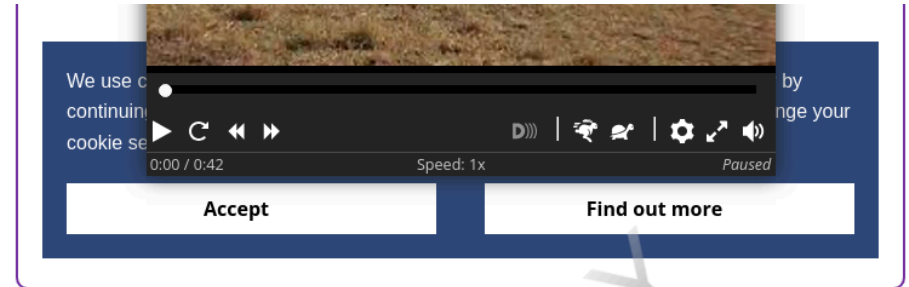


**FIGURE 6.28.** Topi. A male with a female in his territory gives an alarm snort and looks off to the distance.

During the breeding season, males defend individual mating territories from other males. Herds of nonterritorial females roam through male territories selecting mates during their one-day estrus (the sexually receptive, fertile period). A female will visit many territories and can mate multiple times with several males; observers can use this behavior to determine when a female is fertile. Jakob Bro-Jorgensen and Wiline Pangle noticed that males frequently gave alarm calls during visits by estrus females, even when no predators appeared to be nearby (Bro-Jorgensen & Pangle 2010). They proposed that these false alarms “deceive” a female into staying on a male’s territory so that he can obtain additional matings. This **sexual deception hypothesis** predicts that males will give false alarm calls only when an estrus female is in their territory and only when she is trying to leave.

#### Video: Male topi false snorting and then copulation attempt

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To test this hypothesis, the researchers observed the behavior of 53 estrus and 20 non-estrus females between 2005 and 2009 in Masai Mara National Reserve in Kenya. Individuals were identified by their coat color and marking patterns. The researchers recorded the territorial location of the female and all matings, alarm snorts, and departure attempts (i.e., when a female attempted to leave a male’s territory). Following each snort, the researchers scanned the area for predators, which were easy to locate because the habitat was open and topi tend to stare at a predator following a snort alarm. The researchers also recorded all alarm snorts to determine whether true alarm snorts—those

These results are consistent with each of Wheeler's predictions and imply that subordinate capuchins produce inaccurate alarm calls to distract others so that they can gain access to clumped food. Note, however, that such calls were given sparingly, probably because of frequency-dependent selection: subordinates that produce them too often are likely to be ignored.

## 6.5 Communication can involve extended phenotype signals

### Learning Objectives

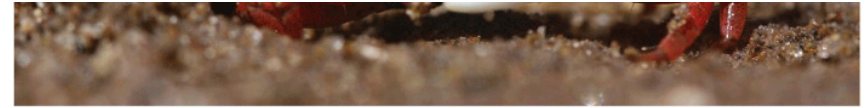
After reading this section, you should be able to

- describe an extended phenotype signal and
- provide one example of an extended phenotype signal.

As we've seen, most communication involves signals associated with an organism's morphology, behavior, or the chemical pheromones it produces. Another class of signals can also be defined: **extended phenotype signals** are those that are expressed beyond the body of an individual and often include modification of the environment. Many extended phenotype signals are involved in mate choice and include the construction of mud pillars by crabs (Figure 6.34) (Matsumasa et al. 2013), the creation of sand craters by fish (Schaedlin & Taborsky 2006), and the manipulation of pebbles and plant material by birds (Soler et al. 1996).



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**FIGURE 6.34. Extended phenotype.** A sand pillar constructed by male fiddler crabs to attract females.

Extended phenotype signals persist longer than behavioral signals and continue to function in the absence of the signaler (Schaedlin & Taborsky 2009). They are also more flexible than morphological signals because they can be more readily modified with changes in environmental conditions. Most are costly to produce and maintain and so are considered reliable indicators of the phenotype of the signaler. As such, they provide an additional signal to others about the condition of a signaler.

Let's examine two species, bowerbirds and sticklebacks, that illustrate extended phenotype signaling.

### FEATURED RESEARCH Bowerbirds construct and decorate bowers

As noted earlier, male bowerbirds construct elaborate stick structures, bowers, to attract a mate. Males construct and decorate bowers with colorful objects from their environment such as flowers, snail shells, and plastic objects discarded by humans (Figure 6.35). They defend their bower from other males and will steal decorations from a rival, even destroying another male's bower if it is undefended. In addition, males display in front of their bower to attract females, and mating occurs in the structure.



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**FIGURE 6.35. Bowerbird bower.** Males construct stick bowers and decorate them with colorful objects.

Gerald Borgia tested the hypothesis that a bower functions as a signal of male quality (Borgia 1985). He assumed that the quantity of decorations at a bower correlates with male quality. If so, male mating success would be expected to correlate positively with the quantity of bower decorations. He tested this prediction by observing a population of 22 male satin bowerbirds (*Ptilorhynchus violaceus*) over two years in New South Wales, Australia. Borgia quantified the size of each bower, the number of decorations on each male's bower, and the number of copulations the male obtained in his bower.

#### Video: Bowerbird copulation

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Male mating success was highly skewed, with the top-five males obtaining over 50% of the copulations. There were significant positive correlations between mating success and the size of a bower as well as the number of snail shells, blue feathers, and yellow leaves on a bower. These data suggest that bowers function as signals of male quality. These structures require great effort to build, decorate, and defend. Only males in the best condition can elaborately decorate and defend large bowers, and such males appear to be the most attractive to females.

Bowerbirds represent perhaps the most conspicuous example of species with extended phenotype signaling. Many male fish also build nests, and some species add decorations to them to attract females. This is particularly common among sticklebacks, a group of small freshwater fish found throughout the world. Let's look at one example of work that investigated the signaling function of such nest decorations.

#### FEATURED RESEARCH Sticklebacks decorate their nests

Sara Östlund-Nilsson and Mikael Holmlund investigated the function of nest decoration behavior in three-spined sticklebacks (*Gasterosteus aculeatus*) (Östlund-Nilsson & Holmlund 2003). Three-spined stickleback males construct nests of soft algae within a shallow depression in sand. Females lay eggs in a nest, and only the male cares for the eggs. Some males decorate the entrance to the nest with materials that provide a striking color contrast: for instance, males that build a nest with green algae will place a piece of red algae at the entrance, and vice versa.

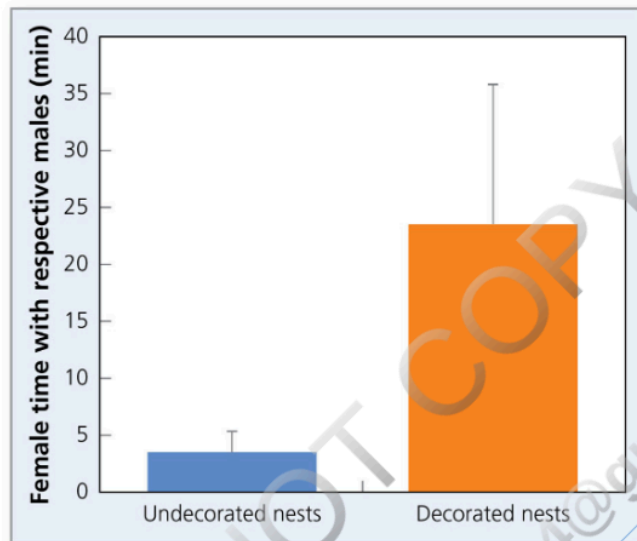
The research team captured individuals from the wild and housed them in individual aquaria. Breeding males were offered green algae and, when they began to construct a nest, an equal number of potential decorations that differed in color and material: red, green, blue, and silver foil sticks as well as red and blue shiny spangles. All males readily added these objects as decorations near the entrance of their nest and showed a strong preference for red sticks.

Given that males used the offered materials as decorations, the researchers conducted a mate choice experiment in which they manipulated the quantity of decorations at a nest. They first matched pairs of males for size, weight, and coloration. Each male was allowed to construct a nest using green algae. Males were then captured and moved to the other nest to control for differences in nest-building behavior. One male was randomly assigned to the "nest decorated" treatment, and the researchers added five red sticks, two red spangles, and two blue spangles to the nest entrance. For the control male, the researchers added one piece of green algae at the nest entrance. Males were then leashed to restrict their movement but could still perform mating displays. A female was allowed to view each male for ten minutes and then interact with the males. The researchers recorded the time spent near each male and whether the female mated with him.

All eight females tested preferred the male whose nest had been decorated. On average, they spent over 80% of the time near the male with the decorated nest (Figure 6.36); the three females that mated did so with the male that had the decorated nest. This study supports the hypothesis that males use contrasting colored objects as extended phenotype signals to attract females. Males will decorate their nest entrance with colored objects that contrast strongly with the color of the nest, and females prefer to mate with males that have decorated nests. Why do females show this preference? If nest decorations are costly to produce and maintain, male quality may correlate



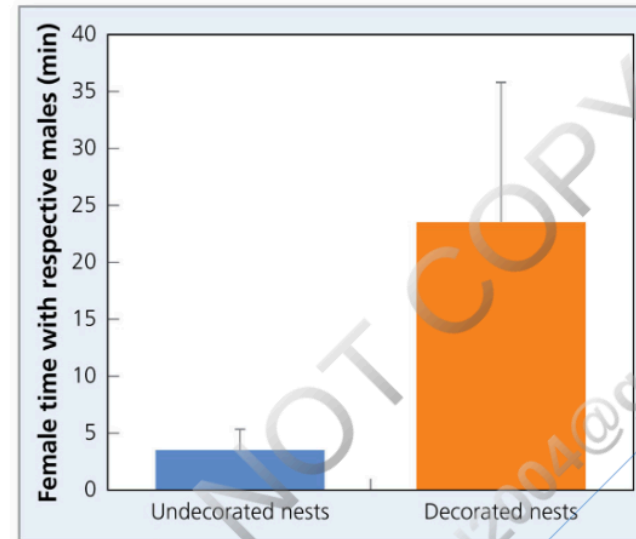
females show this preference: if nest decorations are costly to produce and maintain, male quality may correlate with the extended phenotype signal that he constructs.



**FIGURE 6.36. Female choice of males.** Mean (+SE) time spent with respective three-spined stickleback (*Gasterosteus aculeatus*) males. Females spent more time in front of males with nests containing colored sticks and spangles. (Source: [Östlund-Nilsson & Holmlund 2003](#))

Our discussion of signals to this point has largely assumed that communication occurs between one signaler and one receiver. In many situations, however, other individuals are nearby and so can intercept signals that are produced. We examine the implications of this in the last section of the chapter.

attract females. Males will decorate their nest entrance with colored objects that contrast strongly with the color of the nest, and females prefer to mate with males that have decorated nests. Why do females show this preference? If nest decorations are costly to produce and maintain, male quality may correlate with the extended phenotype signal that he constructs.



**FIGURE 6.36. Female choice of males.** Mean (+SE) time spent with respective three-spined stickleback (*Gasterosteus aculeatus*) males. Females spent more time in front of males with nests containing colored sticks and spangles. (Source: [Östlund-Nilsson & Holmlund 2003](#))

Our discussion of signals to this point has largely assumed that communication occurs between one signaler and one receiver. In many situations, however, other individuals are nearby and so can intercept signals that are produced. We examine the implications of this in the last section of the chapter.

## 6.6 Communication networks affect signaler and receiver behavior

### Learning Objectives

After reading this section, you should be able to

explain how individuals can benefit by intercepting signals communicated between

- explain how individuals can benefit by intercepting signals communicated between others and
- describe the “audience effect” and provide one example.

While the simplest communication system involves two individuals, signals can also be intercepted by others. These **bystanders, or eavesdroppers**, are present but do not take part in the signaling (Matos & Schlupp 2005). In such **communication networks**, eavesdroppers can benefit by learning about the presence of competitors or predators. Not surprisingly, eavesdropping is a widespread phenomenon (Valone 2007). In turn, the presence of bystanders can also influence the behavior of signalers, a phenomenon known as an **audience effect**.

We first examine two studies of eavesdropping and then end the chapter by illustrating one example of an audience effect.

## FEATURED RESEARCH Squirrel eavesdropping

In the autumn and early winter, Eastern gray squirrels (*Sciurus carolinensis*) frequently **cache** (or store) food items like nuts for later retrieval. Food caches, however, are subject to pilfering: conspecifics or heterospecifics can steal food. In the deciduous forests of eastern North America, squirrels live with many potential cache pilferers, including other squirrels and birds. Blue jays (*Cyanocitta cristata*) also make food caches and retrieve them by remembering visual landmarks around the cache location (Bednekoff & Kotrschal 2002). Given that these species both cache and live in the same area, Kenneth Schmidt and Richard Ostfeld wondered whether squirrels might eavesdrop on the vocal communication signals of potential cache pilferers to learn about their proximity. A jay that observed a squirrel caching food could easily remember its location and return later to pilfer the contents. The researchers hypothesized that squirrels might alter their feeding preferences for different food items depending on whether jays were nearby or too far away to watch. They predicted that when jays are nearby, squirrels should reduce their preference for feeding on cacheable food items that could be stolen after being cached.

### Video: Squirrel eavesdropping on jay call

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To test this prediction, Schmidt and Ostfeld established pairs of food patches in eastern New York in early winter (Schmidt & Ostfeld 2008). Each food patch was filled with pea gravel and 15 hazelnuts. One patch contained unshelled hazelnuts, while the adjacent tray contained shelled hazelnuts. Squirrels frequently cache intact hazelnuts but rarely cache nuts without shells, presumably because unshelled nuts cached in the ground rot quickly. Food items were mixed into the pea gravel, forcing squirrels to dig through the gravel to find them. The first few nuts were relatively easy to find, but food discovery then became more and more difficult. This design ensured that a squirrel would leave a patch before all the food was found, because the last few items would be very difficult to acquire. The number of food items left, called the giving-up density (GUD), indicated how much effort the squirrel allocated to feeding in that patch (see Chapter 8).

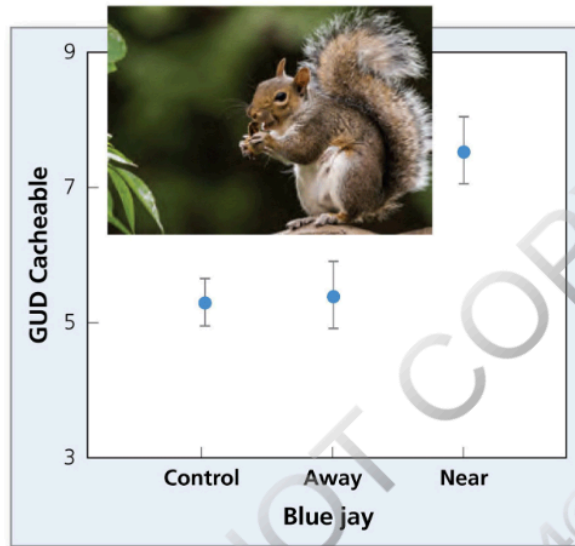
Jays use vocalizations to communicate with conspecifics to defend territories and attract mates. Can squirrels use jay vocalizations to assess the threat of pilfering? Schmidt and Ostfeld recorded the number of nuts left in each patch for three experimental treatments: (1) blue jay vocalizations from nearby speakers (less than 25 m away); (2) blue jay vocalizations from far-away speakers (more than 125 m away); and (3) vocalizations of other common nonpilfering birds, such as northern cardinals (*Cardinalis cardinalis*) (control group). Food patches were available to the squirrels all day. At the end of each day, the researchers collected all the nuts that remained in each tray, the GUD.

In each case, squirrels consumed the same number of noncacheable nuts per food patch. However, significantly more cacheable nuts were left in the patch when jay vocalizations were played nearby (Figure 6.37). These results suggest that squirrels eavesdrop on heterospecific blue jay vocalizations to learn the birds' presence and location.

When jays appear to be nearby, squirrels reduce the amount of effort they devote to acquiring cacheable food,

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When jays appear to be nearby, squirrels reduce the amount of effort they devote to acquiring cacheable food, presumably because it is more likely to be pilfered if cached.



**FIGURE 6.37. Giving-up densities of cacheable food.** Mean ( $\pm$  SE) giving-up density (GUD) of cacheable food items for each treatment. Squirrels left more cacheable nuts (higher GUDs) when jay vocalizations were played nearby than when vocalizations were played far away or for controls. Inset: gray squirrel. (Source: [Schmidt & Ostfeld 2008](#))

We just saw how receiver behavior was affected by eavesdropping within a communication network. Signalers are also affected by the presence of bystanders, as demonstrated in the audience effect we see next.

## FEATURED RESEARCH Audience effects in fighting fish

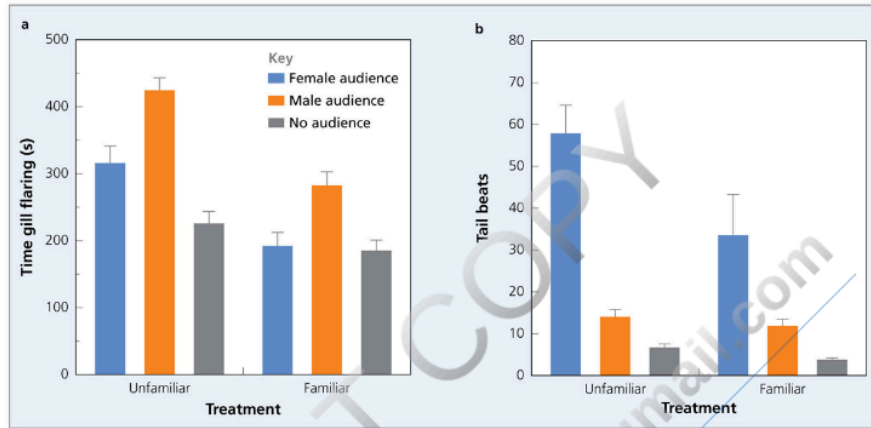
Teresa Dzieweczynski, Courtney Gill, and Christina Perazio investigated how a bystander affects male-male interactions in male fighting fish (*Betta splendens*) ([Dzieweczynski, Gill, & Perazio 2012](#)). As we discussed earlier in this chapter, male fighting fish are highly aggressive and compete for territories and mates. Males use stereotypical display signals, flaring of the gill covers and tail beats, in both male-male interactions and when interacting with females. The team asked two questions: how does the sex of the audience affect male display behavior, and how does familiarity with an opponent influence male display behavior? In many species, signaler behavior can be influenced by an audience ([Zuberbühler 2008](#)) but the influence of familiarity is less clear. However, the **dear enemy hypothesis** ([Temeles 1994](#)) predicts that individuals will show reduced aggressive interactions with familiar individuals, compared to strangers who represent a greater threat. The research team investigated both effects.

The researchers designed a simple experiment that examined the aggressive behaviors of a focal male as it interacted with a familiar or unfamiliar opponent male when a female, male, or no bystander was present. The focal male and its opponent, both of which were closely matched for size and color, were placed in adjacent tanks, separated by a removable opaque partition. For males assigned to the “familiar opponent” treatment, the divider was removed and the males were allowed to interact for ten minutes, after which time the partition was replaced for several hours.

To examine the audience effect, an audience tank was placed in front of both opponent tanks and contained a female bystander, a male bystander, or no



with a female audience present, which may be because tail-beating behavior has a higher prevalence in courtship behavior than gill flaring (Figure 6.39).



**FIGURE 6.39. Aggressive behavior.** Mean (+ SE) (a) time with gills flared and (b) number of tail beats by focal males towards familiar and unfamiliar opponents in the presence of a female audience (blue bar), male audience (orange bar), or no audience (gray bar). (Source: [Dzieweczynski, Gill, & Perazio 2012](#))

These results demonstrate that signaling behavior can be affected by the presence of an audience. Males used more conspicuous aggressive displays (erect gill covers) when a male audience was present in both the familiar and unfamiliar opponent treatments. A male audience represents a greater competitive environment, and males apparently respond with an increased aggressive display. The presence of a female audience elicited more courtship-related behaviors (tail beats), indicating that both social context and audience effects are important components of the communication network for this species.

Many animals live in complex social environments surrounded by both conspecifics and heterospecifics. This variation creates the opportunity for individuals to acquire information from others by intercepting their signals, but also can affect signal production. Much work has focused on understanding how and when such audience effects influence signaling behavior.

## CHAPTER REVIEW

### 6.1 Communication occurs when a specialized signal from one individual influences the behavior of another

- A signal is an evolved trait, while a cue is a consistent aspect of the environment that can guide behavior.
- The honeybee waggle dance is a behavioral signal indicating the location of food.
- Alarm calls are common vocal signals.

### 6.2 The environment influences the evolution of signals

- Selection should favor signals that travel most readily through a particular environment, and that are easy for receivers to detect.
- Ant foraging behavior is affected by temperatures that degrade their chemical signals.
- Fish courtship display effectiveness is affected by background environmental properties.
- Bowerbird vocal-signal frequencies vary with habitat structure.

### 6.3 Signals often accurately indicate signaler phenotype and environmental conditions

- Signals will be accurate indicators of conditions when the fitness interests of the signaler and receiver are similar, they cannot be faked, and are costly to produce.
- Aposematic coloration in frogs, courtship displays in spiders, and opercular displays in fish are examples of honest signals.

### 6.4 Signals can be inaccurate indicators when the fitness interests of signaler and receiver differ

- Inaccurate signals can evolve when the fitness interests of signaler and receiver differ.
- Visual morphological signals in salamanders and fangblenny fish are examples of dishonest signals.
- Topi and capuchins produce dishonest vocal alarm signals.

### 6.5 Communication can involve extended phenotype signals

- Extended phenotype signals are expressed

### extended phenotype signals

beyond the body of an individual.

- Fiddler crab sand pillars and bowerbird and fish nest decorations are extended phenotype signals.

### 6.6 Communication networks affect signaler and receiver behavior

- Third-party bystanders can eavesdrop on the signals between a signaler and receiver.
- Squirrels eavesdrop on blue jay vocal signals.
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## CHAPTER 5

# Sensory Systems and Behavior

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 5.1 [Animals acquire environmental information from their sensory systems](#)
- 5.2 [Chemosensory systems detect chemicals that are perceived as tastes and odors](#)
- 5.3 [Photoreception allows animals to detect light and perceive objects as images](#)
- 5.4 [Mechanoreceptors detect vibrations that travel through air, water, or substrates](#)
- 5.5 [Some animals can detect electric or magnetic fields](#)
- 5.6 [Predator and prey sensory systems coevolve](#)

### Features

- |                        |  |
|------------------------|--|
| Scientific Process     | 5.1 <a href="#">Antlion mechanoreception</a>                   |
| Applying the Concepts  | 5.1 <a href="#">How do mosquitoes find their victims?</a>      |
| Quantitative Reasoning | 5.1 <a href="#">Hummingbird hawkmoths and sugar preference</a> |

As we headed out for a walk one warm night in Tucson, Arizona, we noticed that the front porch light was surrounded with hundreds of insects. Unexpectedly, our dog Grace moved toward a large animal sitting under the light: a Sonoran desert toad (*Incilius alvarius*) (Figure 5.1). These toads have skin glands that produce a potent toxin strong enough to kill a dog, so we kept Grace far away from it. Toads prefer moist environments, but the concentration of insects around the light had drawn it to our dry concrete patio.



**FIGURE 5.1. Sonoran desert toad.** This nocturnal toad feeds on a variety of invertebrates, including those attracted to artificial lights.

Many nocturnal insects, especially moths, are strongly attracted to artificial lights with a high ultraviolet (short-wavelength) component. When scientists collect nocturnal insects, they often shine a bright ultraviolet light on a white sheet to attract them. Exactly why nocturnal insects are attracted to such lights is not yet fully understood. Whatever the explanation, inventors have profited from the knowledge that moths' eyes are less sensitive to longer wavelengths of light: specially designed "bug lights" that do not emit ultraviolet wavelengths attract fewer moths (van Langevelde et al. 2011). Replacing our standard light bulb with one of these has eliminated the problem of attracting so many insects (that in turn attract poisonous toads) to our patio.

In this chapter, we examine how animals perceive their environment. We begin with a basic overview of the nervous system as a proximate link between the environment and behavior. We then examine specific sensory systems that allow animals to detect various types of environmental information, focusing on chemicals, light, and sounds. Next, we illustrate differences between human sensory perception and that of several other taxa by examining how animals detect electric and magnetic fields. Finally, we investigate coevolution in sensory systems between species that interact, and we see that species' sensory systems evolve in response to the behavior of other species.

Two important themes run through this chapter. The first is that researchers need to understand how animals perceive their environment in order to understand their behavior. The second is that animals living in the same environment may perceive it very differently based on differences in their sensory systems.

### Video: Sonoran toads pose danger for dogs

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Video: Sonoran toads pose danger for dogs

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### 5.1 Animals acquire environmental information from their sensory systems

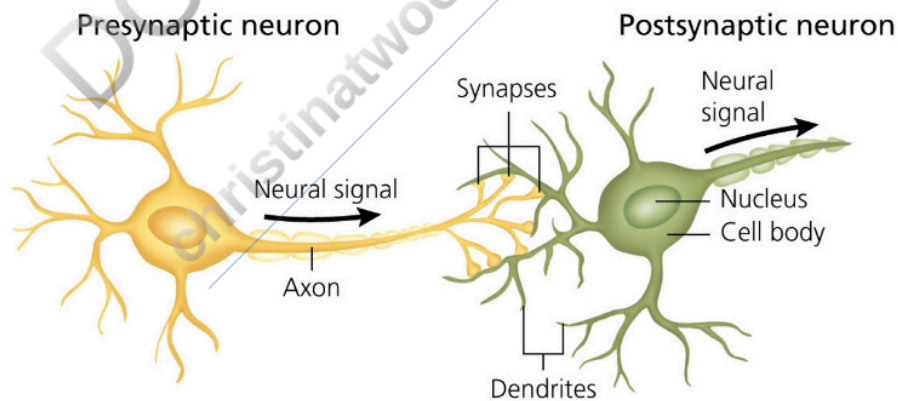
## Learning Objectives

After reading this section, you should be able to

- describe the “umwelt” of a species and
- describe how neurons transmit information from sensory receptors.

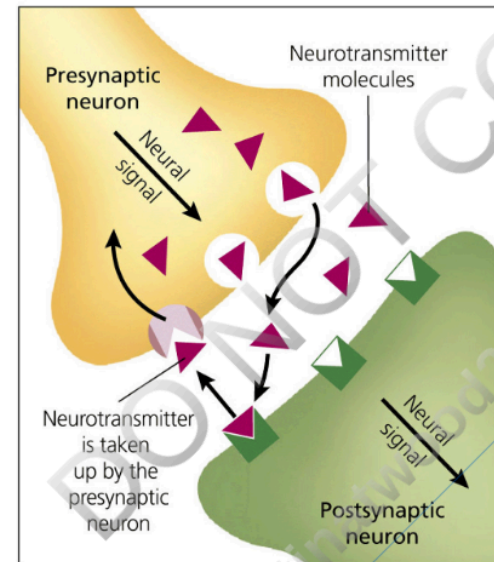
Animals live in a heterogeneous world that varies continuously. Abiotic environmental factors such as light intensity, moisture, and temperature vary widely across space and over time, as do biotic parameters such as the availability of food and mates and the presence of competitors and predators. Such environmental heterogeneity can negatively affect the fitness of individuals that cannot respond appropriately to different environmental conditions.

Environmental information comes in many forms, such as chemical compounds, mechanical sound waves and electromagnetic (light) waves, magnetic fields, and even electrical fields. Animals assess current conditions by gathering information about the environment via their sensory systems, which include sensory organs and receptors that have evolved to acquire this information. Sensory receptors are nerve endings that respond to environmental stimuli and transmit information via neurons, nerve cells that receive and transfer electrical and chemical signals. Neurons are composed of three parts: many dendrites that detect a stimulus; a cell body (or soma), where the information is integrated; and an axon, which conducts the electrical signal to the axon terminal, where it can be transmitted to other neurons, organs, or muscles and affect behavior (Figure 5.2).



**FIGURE 5.2. Neuron.** The different parts of a neuron. The neural signal travels from the presynaptic to the postsynaptic neuron.

Neurons usually have a polarity, so information travels in only one direction. Receptors respond to the energy in a specific environmental stimulus by opening ion channels in the cell membrane that allow an influx of ions. The result is a change in ion concentration inside and outside the cell that leads to a difference in electrical voltage across the membrane. When the difference in electrical charge reaches a specific threshold, an action potential is generated that travels along the axon until it reaches the end; once there, it can cause the release of neurotransmitters, such as serotonin, into the synapse, the gap between two neurons. The neurotransmitters travel across this gap and interact with the postsynaptic nerve cell membrane, which can cause its ion channels to open and initiate another action potential in that neuron (Figure 5.3). Subsequently, the neurotransmitters are reabsorbed by the presynaptic neuron. This process continues as action potentials travel from neuron to neuron and to different cells. Action potentials that travel to muscles can cause them to contract, resulting in behavior.

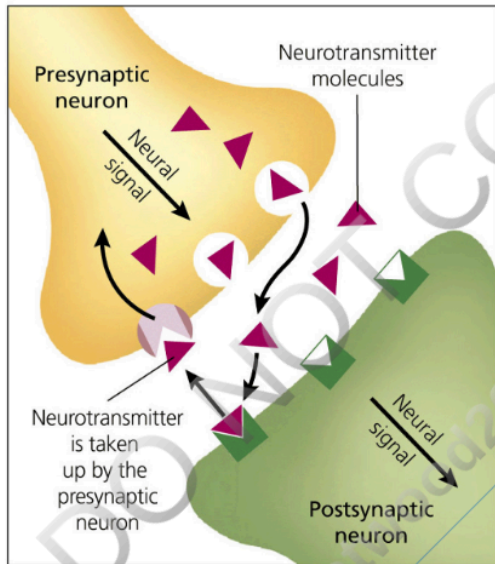


**FIGURE 5.3. Synapse.** The movement of neurotransmitters across the synapse. Electrical signals are transformed into chemical signals that move across the synapse.

Because species have very different types of biotic interactions, unique evolutionary histories, and may live in different environments, the information that is most important to one species may differ substantially from what is most important to another. As a result, we see tremendous variation in the sensory capabilities of different species. A consequence is that each species will have its own specific perceptual environment, or “umwelt” (Von Uexküll 1909).

Throughout this chapter we illustrate important aspects of how animals detect environmental information from their sensory systems. We start by examining the most widespread sensory system: chemoreception.

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## 5.2 Chemosensory systems detect chemicals that

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## are perceived as tastes and odors

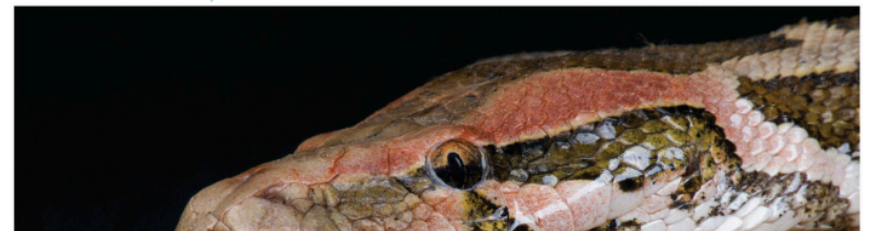
### Learning Objectives

After reading this section, you should be able to

- distinguish between pheromones and odorants,
- differentiate between gustation and olfaction, and
- explain how researchers use behavioral and physiological responses to assess the chemosensory capabilities of animals.

The most primitive and universal sensory system is **chemoreception**, the detection of chemical stimuli. Even single-celled organisms such as bacteria can detect and respond to these stimuli (e.g., MacNab & Koshland 1972). In multicellular organisms, chemoreception includes **gustation** (taste), the detection of dissolved chemicals known as tastants, and **olfaction** (sense of smell), the detection of water- or airborne chemicals known as odorants and pheromones. General **odorants** are not species-specific and allow animals to locate food and avoid environmental dangers such as predators and fire. **Pheromones**, by contrast, are species-specific organic compounds produced by an individual that affect the behavior of another individual of the same species and typically elicit a specific reaction when detected. They can provide information about the presence of a conspecific food trail, alarm cues indicating predators, or the sex of an individual as a potential mate (see Chapter 6). Sometimes, however, it can be difficult to distinguish whether a particular chemical stimulus is species-specific; in such cases, the stimuli are called odorants until more is known about their specificity.

At its most basic, the chemosensory system involves the binding of a discrete chemical molecule to a receptor on the surface of a sensory neuron. As we discussed, that binding generates an action potential that is propagated to the central nervous system. Animals detect chemical compounds via odor-binding proteins in sensory structures such as antennae (for invertebrates) and oral and nasal cavities (for vertebrates) (Firestein 2001). Many species facilitate chemical perception by increasing the movement of air or water over their sensory receptors once a chemical has been discerned. This behavior takes the form of sniffing (mammals), tongue flicking (reptiles; Figure 5.4), and enhanced ventilation of water (aquatic species) or air (terrestrial invertebrates). As we will see, researchers often use such behaviors to characterize when a particular chemical has been detected.



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**FIGURE 5.4. Snake tongue flick.** Reptiles, like this snake, flick their tongues to detect chemical odorants in the air.

We can begin to assess the chemosensory capabilities of different species by simply characterizing the diversity of chemoreceptors present in a species. One avenue of research has examined the number of odorant receptor genes across taxa, which varies widely. For instance, there are about 130 odorant receptor genes in the fruit fly (*Drosophila melanogaster*), 400 in humans, 1,100 in mice, over 1,200 in the roundworm (*Caenorhabditis elegans*), and almost 2,000 in the African elephant (*Loxodonta africana*) (Bargmann 2006; Nijmura, Matsui, & Touhara 2014). Presumably, variation in receptor types is correlated with chemosensory capability, but this relationship is still being examined.

A more direct method of study is to record behavioral or physiological responses to the experimental presentation of stimuli. A response is interpreted as an ability to detect the chemical. Examples from rodents and cuttlefish illustrate how researchers use behavioral and physiological responses to understand the chemosensory capabilities of animals.

## FEATURED RESEARCH Sweet and umami taste perception in rodents

Many animals use olfaction to locate food and gustation to determine its quality (e.g., its nutritional value and potential toxicity). There are five basic tastes—sweet, umami (a form of savory taste), salty, sour, and bitter (Chandrasekar et al. 2006)—and each gives animals different types of information about food (Temussi 2009). For example, sweet tastes provide information about energy content by indicating the presence of carbohydrates, including sugars. Umami tastes provide information about amino acids, the compounds that comprise proteins. Salty tastes can help animals identify salts that allow them to maintain electrolyte balance. Sour and bitter tastes can help animals avoid potentially toxic substances.

Grace Zhao and her colleagues investigated how mammals perceive sweet and umami, the two main attractive taste modalities for many animals, including humans (Zhao et al. 2003). In mammals, the oral cavity contains numerous taste buds, clusters of different types of neuroepithelial taste cells. Receptor taste cells contact the external environment in the oral cavity and contain G-protein-coupled receptors (GPCRs) that bind to sweet,

umami, bitter, or umami compounds; such binding initiates a signaling cascade that releases neurotransmitters to nearby afferent neurons that send signals to the brain. The research team focused on three candidate GPCR subunits (T1R1, T1R2, and T1R3) that were known to form two heterodimer receptors (T1R1+T1R3 and T1R2+T1R3). Prior work suggested that T1R1+T1R3 mediated umami taste while T1R2+T1R3 functioned as

## 5.3 Photoreception allows animals to detect light and perceive objects as images

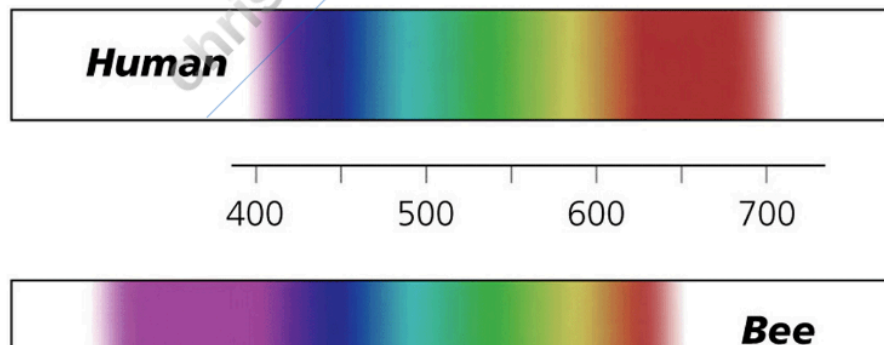
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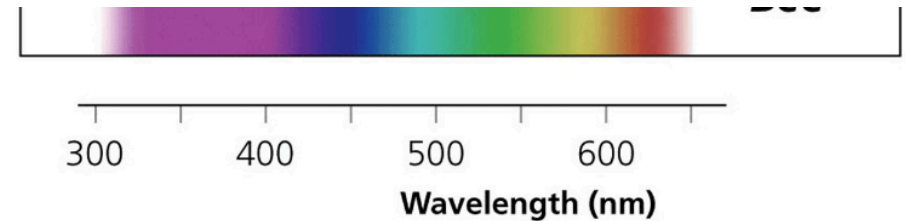
- differentiate between rod and cone photoreceptors and
- describe how researchers examine the photoreceptive ability of an organism.

Wavelengths of light—electromagnetic radiation in various frequencies—can be absorbed by, reflected by, or refracted off objects in the environment. Photoreception is the ability to perceive light and physical objects; it results from visual sensory systems detecting electromagnetic radiation. Vision receptors, or **photoreceptors**, contain photosensitive opsins, proteins that change shape when struck by light and change the permeability of photoreceptor neurons, generating action potentials. Variation in opsin structure confers sensitivity to different wavelengths of light (Stevens 2013). Photoreceptors also vary in their sensitivity to light intensity. For example, in vertebrate eyes, there are two types of photoreceptors: **rods**, which are highly sensitive to a wide spectrum of light at low levels of illumination, and **cones**, which are sensitive to a narrower range of wavelengths of light and thus color perception.

Across taxa, we see great variation in the number and types of photoreceptor cells. There is a correspondingly wide variation in the wavelengths of light that animals can detect. Most species appear to have either three or four types of photoreceptor cells, but these can have very different sensitivities to light frequencies. Human eyes can detect wavelengths between 380 and 690 nm, a range known as visible light. Many species of insects, birds, reptiles, and amphibians can detect wavelengths outside this range (Figure 5.8).



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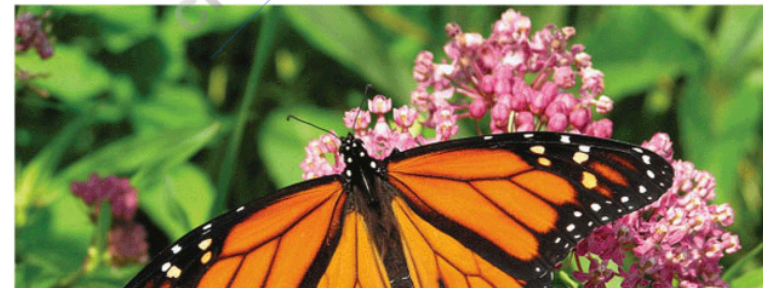
**FIGURE 5.8.** Light wavelengths visible to humans versus those visible to bees. Species differ in their ability to detect certain wavelengths of light. Note that bees can detect ultraviolet wavelengths that humans cannot.

Let's consider three examples that illustrate how researchers study the visual sensory system Umwelt of different species.

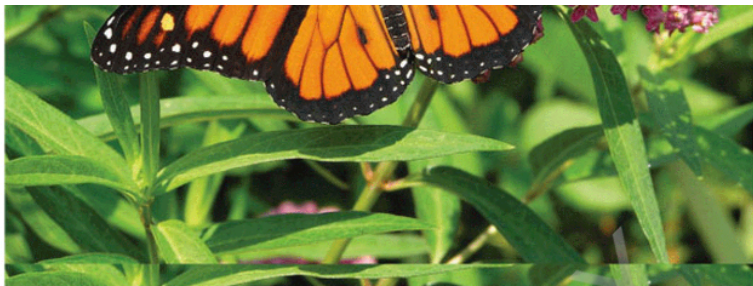
### FEATURED RESEARCH Color vision in monarch butterflies

Many animals make extensive use of color information about their environment, especially when foraging or selecting a mate. One group that has a very wide range of light perception capabilities is butterflies, which have compound eyes containing three opsins that detect ultraviolet, blue, and red-orange wavelengths (Stalleicken, Labhart, & Mouritsen 2006). However, the presence of these opsins does not necessarily indicate the ability to perceive and discriminate among these wavelengths (i.e., true color vision). That requires the ability to discriminate among different wavelengths, independent of the intensity of light (Kelber, Vorobyev, & Osorio 2003).

Douglas Blackiston, Adriana Briscoe, and Martha Weiss used behavioral assays to determine whether monarch butterflies (*Danaus plexippus*) (Figure 5.9) have true color vision (Blackiston, Briscoe, & Weiss 2011). They trained individuals to associate a specific color (red, purple, blue, or yellow) with a food reward by allowing them to feed from an artificial flower of a specific color. After eight days of training, each butterfly was placed in a cage with an array of 20 artificial flowers: 19 were different intensities of gray (in even incremental shades from nearly black to almost white), and one flower was the color that the butterfly was trained on. This flower was closely matched for reflectance (light intensity) with one or two of the gray flowers, thus ensuring that the light intensity of both types was similar but that the wavelengths reflected off of them differed.



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**FIGURE 5.9.** Monarch butterfly. An insect with true color vision.

Blackiston and his colleagues measured the time individuals spent probing each flower in the array. The results showed that the butterflies probed the colored flower they were trained on significantly more than the gray flower with similar reflectance. In fact, they spent more than 95% of their time at the flower with the color they were trained on. The performance of individuals trained on four different colors demonstrates that monarch butterflies have the ability to detect a wide range of colors. This adaptation could allow them to track changes in nectar availability in the different flowers found in their summer and winter habitats.

#### Video: Trained monarch in flight

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## FEATURED RESEARCH Ultraviolet plumage reflectance in birds

In many birds, females select a mate based on the male's plumage characteristics. For instance, female house finches (*Carpodacus mexicanus*) prefer to mate with males that have the greatest amount and intensity of red coloration in their plumage (Hill 1990). But in other species, such variation in male plumage does not appear to affect female mate choice. Consider the pied flycatcher (*Ficedula hypoleuca*), a small cavity-nesting bird common throughout Europe (Figure 5.10). Male breeding plumage varies in color among individuals, ranging from dull brown to dark black, but previous studies have shown no consistent preference by females for either black or brown males (Alatalo, Lundberg, & Sundberg 1990; Sætre, Dale, & Slagsvold 1994; Sætre et al. 1997).



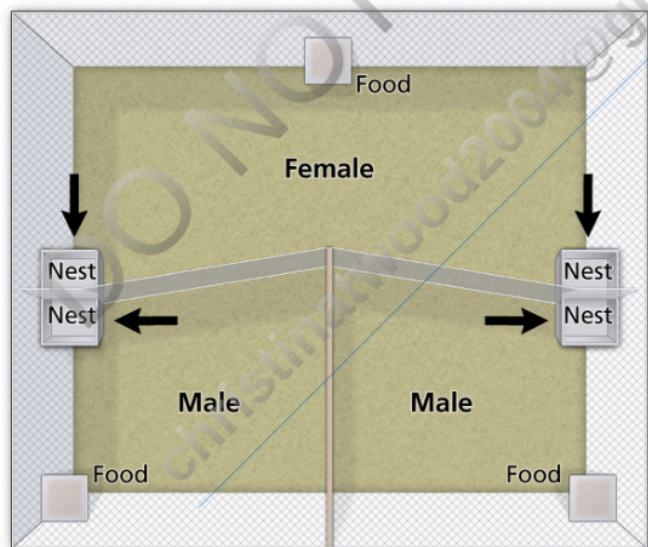




**FIGURE 5.10. Male pied flycatcher.** Males vary in plumage color, ranging from brown to black, and nest in small cavities or bird boxes.

Recent work, however, indicates that the plumage of many birds reflects ultraviolet (UV) wavelengths (Eaton & Lanyon 2003). Because birds can perceive these wavelengths, they see colors and patterns that humans cannot. One implication of this finding is that many species traditionally categorized as sexually monomorphic are in fact sexually dimorphic because the sexes differ in UV color pattern (Eaton 2005). Another is that variation in male UV plumage traits may affect female mate choice behavior.

Heli Siitari and her colleagues tested the hypothesis that variation in male UV color affects female mate choice in pied flycatchers (Siitari et al. 2002). They captured adults at the beginning of the breeding season and housed them in a large outdoor aviary that had three compartments: one for a female and one for each of two males. The male compartments were separated by plywood, preventing males from interacting. Each male had access to one of two dual-chamber nest boxes, and the female had access to both (Figure 5.11).

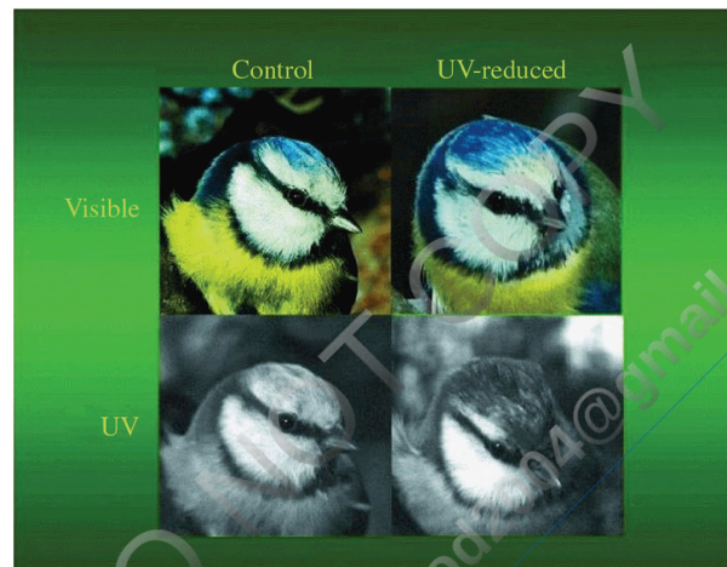


**FIGURE 5.11. Mate choice arena.** Outdoor aviary with three compartments. Females could access each nest box, while each male could only access one. Arrows indicate openings to each nest box. (Source: Siitari et al. 2002)

In each of 13 trials, males were matched for percent black coloration, body size, and UV reflectance of the crown and back. One male was then treated with a mixture of UV-absorbing sunscreen and a waterproofing substance

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that reduced the UV reflectance of his plumage. The other male was the control and was treated with a waterproofing substance that did not reduce the UV reflectance (Figure 5.12). Males were allowed to habituate to the aviary before the female was introduced, after which the experimental and control males exhibited similar levels of courtship display behavior. Siitari and her colleagues then recorded which nest box the female eventually used to construct a nest, an indication of her mate choice.



**FIGURE 5.12. Bird plumage in UV.** Blue tits (*Cyanistes caeruleus*) are another species with a UV-reflectant crown patch used in courtship. The top row is a blue tit photographed in normal light, and the bottom row is a blue tit photographed using UV light. The left column shows the control, while the right column shows the UV-reduced treatment, which reduced the UV reflectance of the crown patch. (Source: Withgott 2000)

The experimental manipulation strongly affected female behavior: 11 of 13 females preferred the control male to the UV-reduced male. Because other plumage color and behavioral traits did not differ significantly between the males, these data strongly suggest that females assess male quality based on plumage UV coloration. As such, the study provides new insight into how females in this species use ultraviolet cues in mate choice.

## FEATURED RESEARCH Infrared detection in snakes

Earlier, we saw that many species can detect electromagnetic wavelengths shorter than those of visible light. In contrast, other species have evolved the ability to detect longer wavelengths, such as those of infrared radiation (700–1000 nm), which is emitted by warm objects and animals.

The ability to detect infrared wavelengths is relatively rare among species but is found in a diverse set of taxa. For

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example, beetles in the genus *Melanophila* possess pit organs on their thorax that are sensitive to infrared radiation. These beetles lay their eggs on trees that have recently been killed by fire, and they are known to approach forest fires from a distance of several kilometers. Fires emit smoke, ash, visible light, and infrared radiation, but the beetles seem to rely exclusively on infrared radiation to detect burning trees (Evans 1964; Schmitz & Bleckmann 1998). More recently, researchers have discovered that vampire bats, which feed on the blood of vertebrates, also possess heat-sensitive pits on their nose. Being able to detect infrared wavelengths is thought to help them locate a vein during feeding (Gracheva et al. 2011). But the animals best known for this ability are pit viper snakes in the subfamily Crotalinae, which use it to ambush warm-bodied endothermic prey.

All crotaline snakes possess facial pit organs containing neuron terminals that detect infrared wavelengths (Figure 5.13). Infrared information is relayed to and processed by the central nervous system, providing a complementary visual system to the one that detects visible light. But how widespread is this system? Can non-crotaline vipers detect infrared radiation?



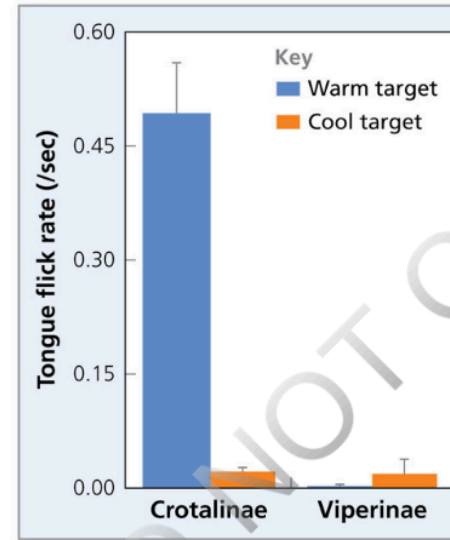
Pit organ

**FIGURE 5.13. Pit organ.** Western diamondback pit viper with an infrared pit organ under the eye.

Adam Safer and Michael Grace compared the infrared detection behavior of two crotaline species (copperhead [*Agkistrodon contortrix*] and Western diamondback [*Crotalus atrox*]) with that of three non-crotaline species of the viperine genus *Bitis* (puff adder [*Bitis arietans*], Gaboon viper [*B. gabonica*], and rhinoceros viper [*B. nasicornis*]) (Safer & Grace 2004). All these snakes hunt mammals whose body temperature typically exceeds ambient temperature. The researchers presented snakes with two white water-filled balloons, each measuring 5 × 9 cm: one was heated to room temperature (20°–25°C) and the other to approximately that of a live mammal (32°–35°C). Both were suspended above the floor at one end of the 95 cm diameter test arena, which had flat black walls.

Individual snakes were placed in the arena and allowed five minutes to acclimate. The balloons (placed 6.5 cm apart) were then introduced 15–20 cm in front of the snake. The researchers recorded tongue flicks, head turns,

approaches, and strikes at each target. They found that the crotaline snakes exhibited a greater number of responses to the warm target than to the cool target (Figure 5.14). These snakes struck the warm target in 10 of 31 trials but never struck the cool target (Safer & Grace 2004). In contrast, the non-crotaline snakes' behavioral responses did not differ with respect to the two targets; these snakes did not strike either in any of the trials.



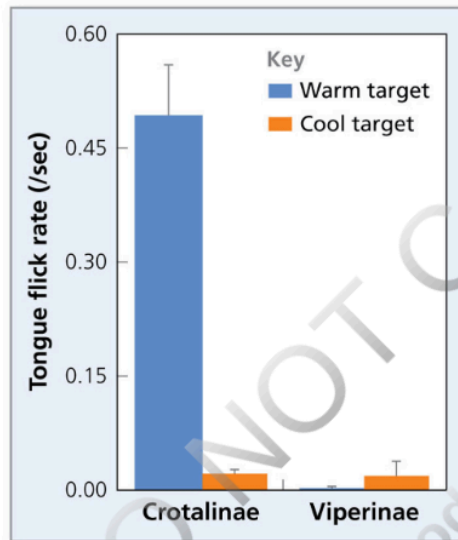
**FIGURE 5.14. Behavioral responses to warm and cool targets.** Mean (+ SE) tongue flick rate. Crotaline snakes exhibited more tongue flicks toward the warm (blue bar) target than the cool (orange bar) target. Viperine snakes exhibited weak responses to both targets. (Source: Safer & Grace 2004)

These data confirm that crotaline snakes detect and respond to warm objects, and potentially animals, differently than they do to cool objects; they can thus perceive differences in infrared radiation. However, this infrared imaging system is not universal among viper species, as demonstrated by the lack of response in the *Bitis* species. The ability to perceive infrared wavelengths provides individuals with additional information about their environment, which can facilitate the detection of both prey and potential threats.

These studies show how researchers have investigated the ability of species to detect and respond to different wavelengths of electromagnetic radiation in the environment. In addition to chemoreception and photoreception, a third source of environmental information is derived from the detection of mechanical waves, as we see next.



Individual snakes were placed in the arena and allowed five minutes to acclimate. The balloons (placed 6.5 cm apart) were then introduced 15–20 cm in front of the snake. The researchers recorded tongue flicks, head turns, approaches, and strikes at each target. They found that the crotaline snakes exhibited a greater number of responses to the warm target than to the cool target (Figure 5.14). These snakes struck the warm target in 10 of 31 trials but never struck the cool target (Safer & Grace 2004). In contrast, the non-crotaline snakes' behavioral responses did not differ with respect to the two targets; these snakes did not strike either in any of the trials.



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These studies show how researchers have investigated the ability of species to detect and respond to different wavelengths of electromagnetic radiation in the environment. In addition to chemoreception and photoreception, a third source of environmental information is derived from the detection of mechanical waves, as we see next.

## 5.4 Mechanoreceptors detect vibrations that travel through air, water, or substrates

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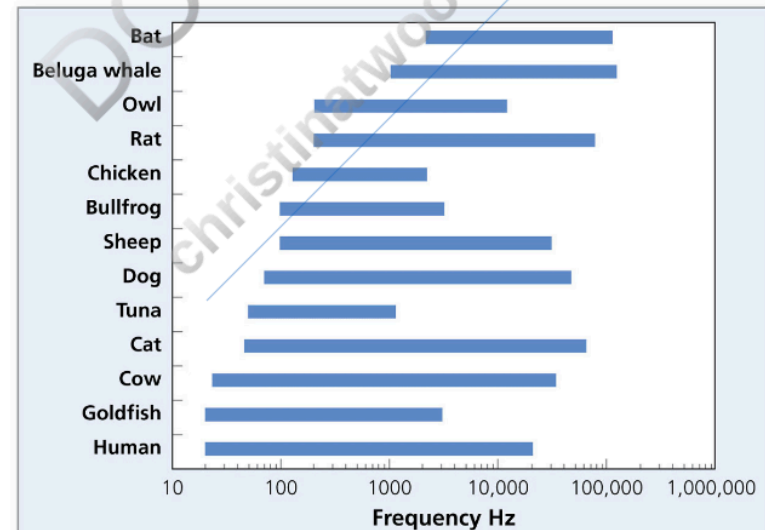
## through air, water, or substrates

### Learning Objectives

After reading this section, you should be able to

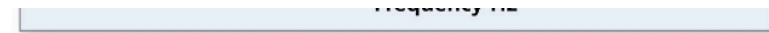
- compare the different types of mechanoreceptors used to detect vibrations on land and in the water and
- describe how mechanoreceptors provide information to individuals about conspecifics and prey.

Sounds, like a bird's song or a lion's roar, are mechanical waves that can be heard. The vibrations of an insect walking on a leaf or the waves made by a fish moving through water are mechanical waves that can be felt. **Mechanoreceptors** allow animals to detect mechanical waves or vibrations that travel through air, water, or physical substrates such as the ground. The sensory structures that detect mechanical waves differ greatly across species. For many terrestrial species, auditory receptors—specialized structures that efficiently gather mechanical waves—are found within ears. These receptors are not always located on the head, however; invertebrate species have them on different parts of their body, including their thorax, wings, or legs. As we saw for photoreceptors, taxa vary greatly in their ability to detect different frequencies (sound waves per second) of mechanical waves (Figure 5.15). Frequencies below the lower limit of human hearing (20 Hz) are known as infrasounds, while those above the upper limit (20 kHz) are called ultrasounds.



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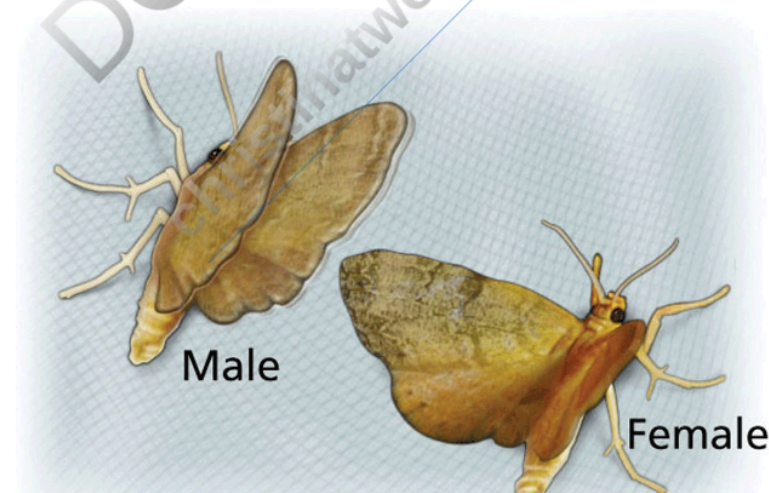
**FIGURE 5.15. Auditory abilities of species.** Species differ in the range of frequencies their auditory system can detect. Each bar represents the range of frequencies detected.

Let's begin our examination of mechanoreception with two examples of sounds that provide information about conspecifics. The first involves the detection of high-frequency sounds in insects, while the second involves the detection of low-frequency sounds in elephants.

## FEATURED RESEARCH Ultrasonic song detection in moths

Insects have one set of mechanoreceptors to detect nearby sounds and others to detect distant sounds. Near-field detectors, such as the Johnston's organ in mosquitoes, are usually sensitive to low frequencies ( $< 100$  Hz). Far-field receptors, such as the tympanal hearing organs found in many insects, are sensitive to a fairly wide range of high frequencies (2–100 kHz), including ultrasounds (Stevens 2013). Thus, insects with far-field receptors can detect the presence of predatory bats that hunt by emitting ultrasounds, as we will see later in the chapter.

In addition, some moth species also produce their own ultrasonic pulses. One explanation for this ability is that they could be used in courtship. Ryo Nakano and his colleagues (Nakano et al. 2006) examined the possible use of such sounds in courtship behavior in Asian corn borer moths (*Ostrinia furnacalis*). The researchers began by recording the courtship songs and behavior of males by releasing a single male and eight virgin females into a small cylindrical mesh cage (5.5 × 5 cm). Males landed near females and quickly began producing courtship songs and behaviors; that is, they raised their wings to an upright position and vibrated them quickly, which produces an ultrasonic pulse (Figure 5.16). Females did not produce any sounds, suggesting that they may use male ultrasonic courtship songs to select a mate.



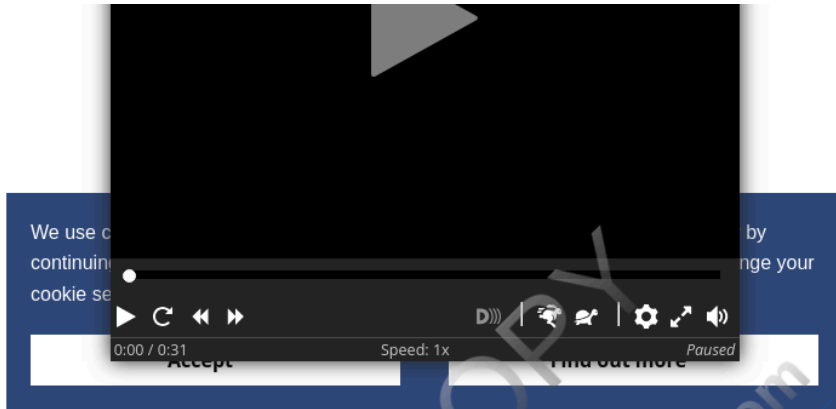
**FIGURE 5.16. Moth courtship.** A male (left) lands near a female (right) and vibrates his wings to produce ultrasonic pulses during courtship. (Source: Nakano et al. 2006)

To examine the role of male ultrasound in courtship, the research team conducted an experiment in which they deafened one group of females by puncturing their tympanal membranes. In control females, no manipulation was done. A sham treatment was carried out on another group of females, in which non-sound-detecting membranes on the leg were punctured. Sham treatments allow individuals to experience the same treatment but without the intended consequences; in this case, the females were not deafened. Individual males in the laboratory were then released into a small flight tunnel 1 m downwind from a small group of either deafened or hearing females, and ensuing courtship and mating behavior was noted.

Hearing females mated within two minutes in 84% of the trials. In contrast, deafened females mated in only 59% of the trials. These data suggest that male ultrasonic pulses are an important component of females' mate choice.

### Video: Male courtship with ultrasonic song production

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### Video: Wing motions during generation of courtship

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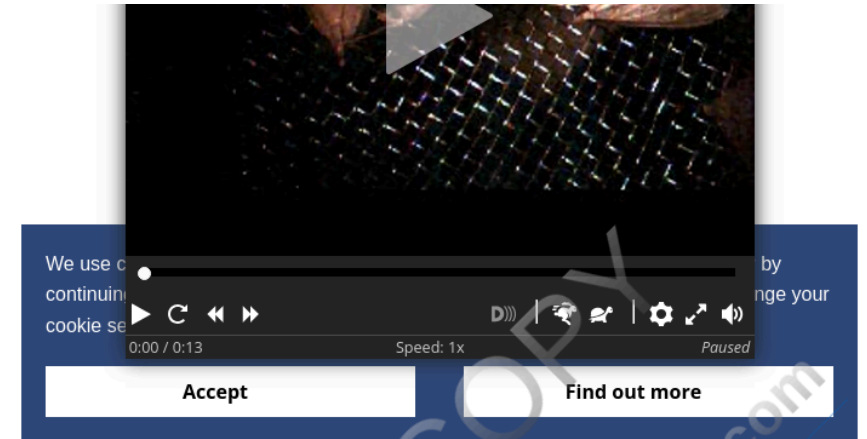
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Video: Wing motions during generation of courtship



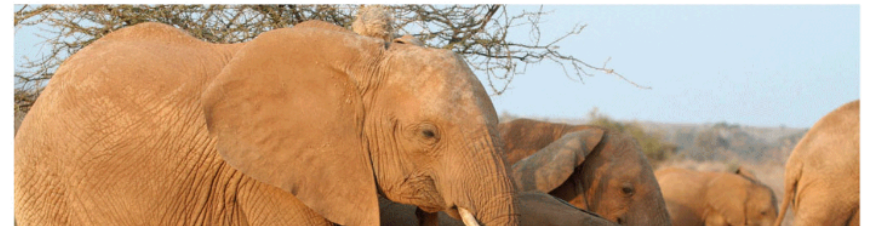
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### FEATURED RESEARCH Long-distance communication in elephants

Many animals use contact calls to maintain associations with others in their social group ([Kondo & Watanabe 2009](#)). For some animals—especially those that live in large, wide-ranging social groups or in habitats with dense vegetation—maintaining visual contact may not be possible. In such circumstances, sounds can be used to maintain contact. But sounds attenuate (lose intensity) as they travel through the environment. How, then, can contact be maintained over long distances? One possibility is using infrasounds, which have very low frequencies and so attenuate more slowly. Several species of large-bodied mammals, including elephants, can produce and detect low-frequency infrasonic sounds.

Elephants live in social groups centered on adult females, which are typically related, and their immature offspring ([Figure 5.17](#)). They produce unique contact calls that are audible to humans to maintain social cohesion, as well as unique low-frequency (< 20 Hz) vocalizations that humans cannot hear. They also exhibit characteristic behaviors in response to hearing a family member's contact call: they move in its direction, producing their own calls. In response to hearing vocalizations of less known, potentially threatening individuals, they tend to bunch into a defensive posture and do not move toward the sound.



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**FIGURE 5.17. African elephants.** Elephants live in social groups.

These differences in behavior allowed Karen McComb and colleagues to determine the distance over which individual African elephants (*Loxodonta africana*) responded to familiar and unfamiliar infrasonic contact calls by playing the calls at different distances (McComb et al. 2003). The work was conducted at Kenya's Amboseli National Park on a population of elephants that had been studied for almost 30 years; thus, all individuals could be recognized and family relationships were known. The team recorded infrasonic contact calls of different elephants on specialized low-frequency digital audiotape. They took advantage of situations when a particular female was absent from a group and played either her contact call or one of a much less familiar elephant. They started at a distance of 2.5 km and noted the individuals' behavior. If no response was detected, they approached the group at 0.5 km intervals and again played the call until they noted a behavioral response. They also measured several behaviors indicative of call detection, including listening (ears held stiff), smelling, or streaming (the production of a new secretion from glands in the forehead). Data were collected for seven different groups over seven years.

Elephants responded to familiar contact calls by producing their own calls or moving in the direction of the call when it was 1.0 km away or closer. The unfamiliar vocalizations elicited a response when played up to 1.5 km away, but individuals never moved toward or produced contact calls in response; instead, they tended to bunch together in a defensive posture. The researchers concluded that infrasounds are used to maintain contact among individuals in their group. The ability to detect long-distance acoustic vocalizations also allows individuals to acquire information about the presence of another, potentially threatening, group while it is still fairly distant.

In these examples, we have seen how the detection of sounds provides important environmental information about the presence of conspecifics. Next, let's examine mechanoreception in water and how it allows some fish to find their prey.

needle, much as they would in response to the presence of actual struggling prey in their pit. Fertin and Casas concluded that such behavioral responses provide clear evidence that antlion larvae detect their prey using substrate-borne vibrations. Antlion larvae possess mechanoreceptor sensilla on their head, legs, and abdomen; further work is required to determine the specific sensory receptors that aid in detecting vibrations made by their prey.

These examples represent different types of information animals gather about their environment by detecting mechanical waves that travel through air, water, and substrates. Next, we examine two less well-known sensory systems: the detection of electric and magnetic fields.

#### Video: Antlion building nest and eating ant

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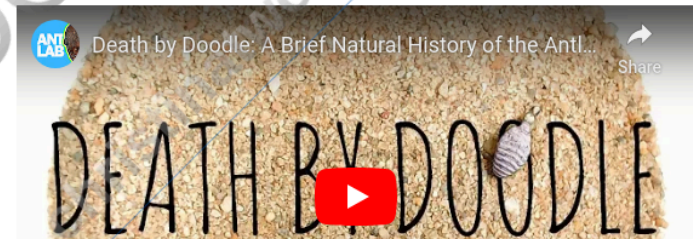
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## 5.5 Some animals can detect electric or magnetic fields

### Learning Objectives

After reading this section, you should be able to

- describe how electroreception is used to identify prey and
- explain how and why selection has favored the evolution of magnetoreception in many species that make long-distance movements.

Some aquatic organisms, such as skates and rays, often need to find buried prey or potential mates. As these buried organisms respire, muscles contract, resulting in the movement of ions that creates a weak electric field. This electric field can be detected in water or moist environments due to the density of the medium (Ruxton 2009).

Other organisms need to determine the appropriate direction for their long-distance movements. The earth's geomagnetic field is made up of electric currents and magnetic materials, and animals can use this field to determine directions. We examine these sensory systems next, focusing first on sharks and then on birds, taxa in which electroreception and magnetoreception, respectively, have been the focus of much research.

### Electroreception

Some species, particularly aquatic ones or animals in moist environments, have evolved **electroreception**, the ability to detect weak electric fields. These species can electrolocate individuals in dark or murky environments or find buried prey. Electroreception is most widespread in elasmobranchs (sharks and rays) but has also been identified in some bony fishes and amphibians, a few mammals (e.g., duck-billed platypuses, echidnas), and some insects.

### FEATURED RESEARCH Sharks detect electric fields

In sharks and rays, electric fields are detected in structures known as ampullae of Lorenzini, a set of pores mostly located on the head that contain a crystalline gel and electrosensitive neurons (Figure 5.20). The presence of an external electric field stimulates these neurons, which then send an electrical impulse to the central nervous system. Electric fields generated by organisms attenuate rapidly in aquatic environments and so can be detected only over distances of a few meters. How have researchers studied electroreception? A typical method is to create

weak electric fields and observe the behavior they elicit.



Ampullae of Lorenzini

**FIGURE 5.20.** Ampullae of Lorenzini on shark head. These structures detect electric fields.

Stephen Kajiura and Kim Holland examined the orientation pathway and attack behavior of naïve juvenile scalloped hammerhead (*Sphyrna lewini*) and sandbar sharks (*Carcharhinus plumbeus*) in response to electric fields that simulated the presence of prey (Kajiura & Holland 2002). The research team investigated the hypothesis that, of the two species, hammerhead sharks have greater electroreception ability due to the enlarged lateral expansion of their head (Figure 5.21). The ability to detect electric fields produced by other organisms would enhance the ability of these predators to locate benthic prey (fishes and crustaceans) buried in the sea floor.

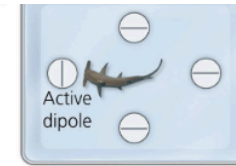
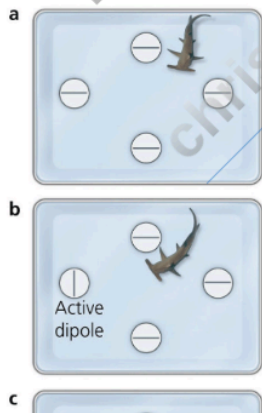




**FIGURE 5.21. Shark heads.** (a) Hammerhead sharks have an enlarged lateral expansion of their head relative to (b) sandbar sharks.

The researchers created a large experimental pen (10 m × 20 m) that enclosed part of a natural reef in Kaneohe Bay, Hawaii. In the shallow part of the pen, the researchers buried a 1 m<sup>2</sup> acrylic plate that contained four dipoles, positive and negative charges separated by a small distance, producing a weak electric field in a specific location. A single shark was introduced into the shallow portion of the pen, and prey odor was released in the center of the dipole array to stimulate food-searching behavior. An individual dipole was then activated, creating a weak electric field that simulated the type produced by a buried prey species. Different dipoles were activated across different trials, and a video camera recorded the sharks' behavior.

Both species oriented toward the active dipole by changing their swimming direction to move closer to it. These changes in orientation occurred when both species were less than 30 cm from the active dipole, and both then attacked it with a bite (Figure 5.22). None of the sharks attacked a nonactive dipole, and all individuals stopped biting an active electrode when the current to it was turned off. These data provide strong evidence that scalloped hammerhead and sandbar sharks orient to weak electric fields and that such fields elicit feeding behavior. However, the researchers found no support for the hypothesis tested because there was no significant difference between the species in the behavioral response thresholds for the weak electric fields used in the experiment. Perhaps hammerheads can detect weaker electric fields than sandbar sharks, but that question requires further study.



**FIGURE 5.22. Shark response to weak electric field.** (a) An individual is swimming before the dipole is active. (b) The dipole is activated (indicated by the vertical line) to produce a weak electric field, and the shark initiates orientation to it. (c) The shark makes a rapid 90° turn to move toward the active dipole. (Source: [Kajlura & Holland 2002](#))

The ability to detect electric fields is a relatively rare sensory ability, but it is an important source of information for a variety of species searching for hidden prey. Next, we examine a sensory system found in a wide variety of taxa that is used to determine direction: the ability to detect magnetic fields.

### Video: Prey-simulating dipole electric field and sharks

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### Video: Prey-simulating dipole electric field and sharks

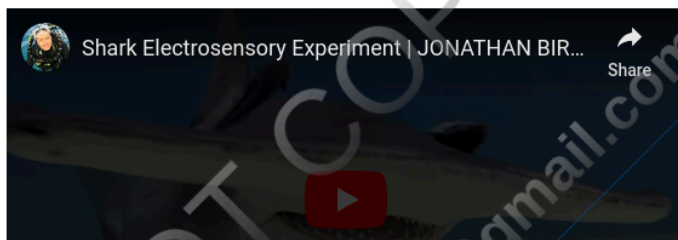
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Video: Shark biologist Dr. Stephen Kajiura from Florida Atlantic University performs an experiment which demonstrates how the electrosensory system of sharks works



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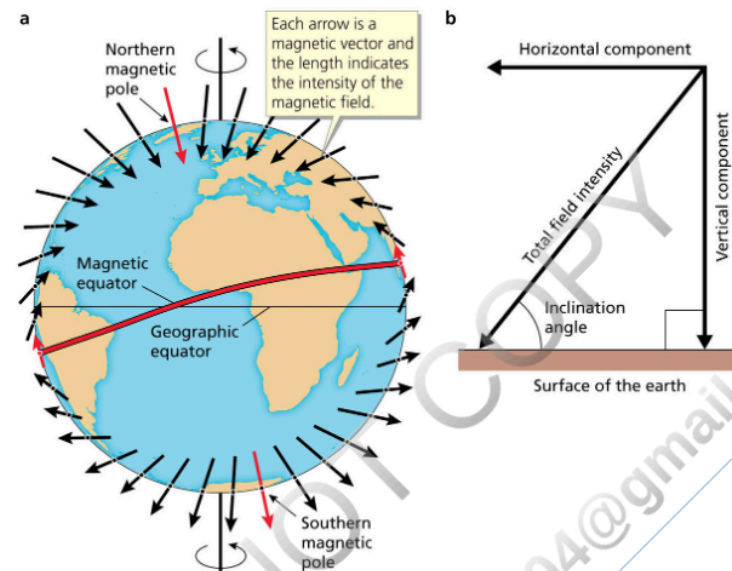
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## Magnetoreception

Many animals migrate long distances, making two-way movements from one location and back each year. To accomplish this, individuals need to determine the appropriate direction to move in different seasons. The earth's magnetic field can provide such directional information (Figure 5.23). **Magnetoreception**, the ability to detect the earth's magnetic field, provides animals with directional information in three ways. First, the magnetic field flows from south to north—it has polarity. Second, magnetic field lines are oriented vertically with respect to the earth's surface at magnetic north and south; at these poles, we can say that the lines have a 90° angle of inclination. These lines become more parallel to the ground as they move toward the magnetic equator, where they have a 0° angle of inclination to the earth's surface. Thus, their angle of inclination with respect to the horizontal varies with latitude. Third, the intensity of the field varies predictably: it tends to be strongest at the poles and weakest at the magnetic equator. Use of a geomagnetic compass has been documented in dozens of species in many taxa, including snails, crustaceans, insects, fish, amphibians, reptiles, birds, and mammals. These behavioral studies have typically examined how manipulations of field direction affect the movement of individuals (e.g., Wiltchko

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have typically examined how manipulations of field direction affect the movement of individuals (e.g., Wiltchko & Wiltchko 2005).



**FIGURE 5.23. Magnetic field of the earth.** (a) The magnetic vectors around the earth. Arrows indicate the local vector and angle of inclination; their length indicates the intensity (strength) of the field. (b) The total field intensity is composed of a horizontal component and a vertical component. (Source: Wiltchko & Wiltchko 2005) (Source: Lohmann, Putnam, & Lohmann 2008)

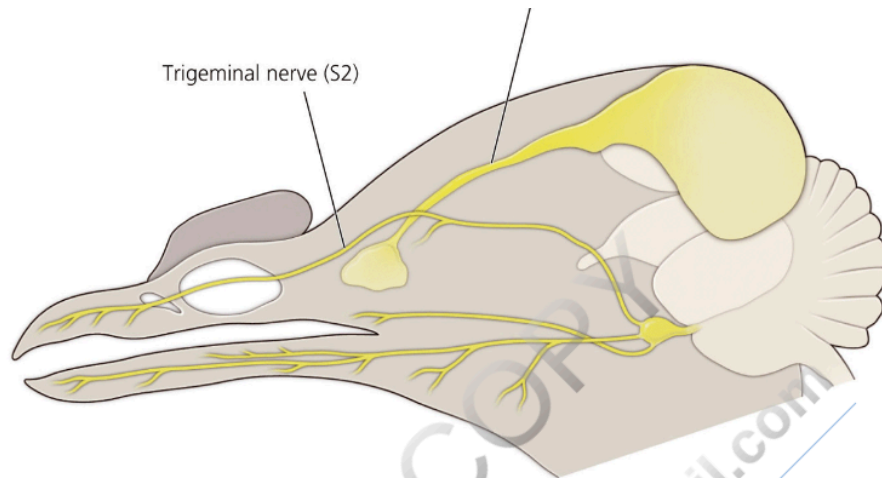
It is less clear how animals detect the earth's magnetic field. Research has focused on two mechanisms. In many animals, certain cells contain crystals of magnetite, a form of iron oxide whose magnetic properties depend on its size and shape. Because crystal magnetite is a permanent magnet, its magnetic field interacts with the earth's magnetic field, creating a force (pressure) that can be detected. Experiments have shown that exposure to external magnetic fields can temporarily disrupt an animal's orientation ability (Wiltchko et al. 1998). More recent work has demonstrated that birds can detect both variation in intensity of an external magnetic field and its direction (Stapput et al. 2008; Wu & Dickman 2012). But where is the magnetic sense located?

Experiments, as well as neurophysiological studies, on a variety of vertebrates have revealed that magnetite appears to be frequently located in the front of the head (Kirschvink, Walker, & Diebel 2001), particularly in the olfactory lamellae of fish and in the upper beak of birds (Diebel et al. 2000; Fleissner et al. 2003). Cordula Mora, Michael Davidson, Martin Wild, and Michael Walker conducted a series of experiments to identify the nerve involved in transmitting magnetic information to the brain in birds (Mora et al. 2004). They focused on two candidate nerves in the upper beak, the olfactory and the ophthalmic branch of the trigeminal (Figure 5.24).

Olfactory nerve (S1)

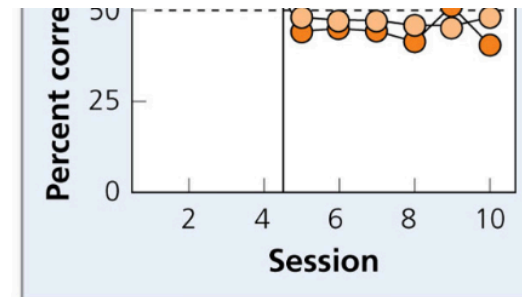
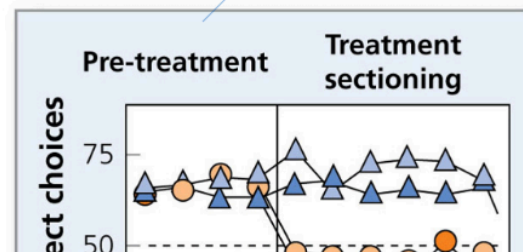
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**FIGURE 5.24. Lateral view of pigeon head.** The olfactory nerve (S1) carries nerve impulses from the olfactory mucosa to the brain, while the trigeminal nerve (S2) carries nerve impulses from the upper beak to the brain. S1 and S2 were sectioned in the two treatments. (Source: [Mora et al. 2004](#))

Mora and her colleagues trained captive pigeons to discriminate the presence or absence of an induced magnetic anomaly in an experimental chamber. The researchers used a magnetic coil to create a magnetic field that was substantially different in intensity and angle of inclination from the typical background field. Four pigeons were trained to move to one feeder if the anomalous magnetic field was present but to move to the other feeder if the background magnetic field was present. If birds made the correct choice, they were rewarded with food. After 24 consecutive training sessions, individuals selected the correct feeder almost 70% of the time, indicating the ability to detect the anomalous magnetic field. Next, the research team cut the ophthalmic branch of the trigeminal nerve in half the subjects and the olfactory nerve in the others. Those with impaired olfactory nerves continued to make the correct choice about 70% of the time, whereas those with impaired trigeminal nerves made the correct choice only 50% of the time ([Figure 5.25](#)). Thus, magnetite in the upper beak appears to provide information about magnetic field intensity and inclination that is then transmitted to the brain via the ophthalmic branch of the trigeminal nerve. These results provide strong support for the hypothesis that magnetite in the upper beak is involved in magnetoreception in pigeons.



**FIGURE 5.25. Percentage of correct choices in four pigeons.** Individuals with a sectioned olfactory nerve (triangles) continued to make a high level of correct choices. Those whose trigeminal nerve was sectioned (circles) exhibited a significant decline in their performance. (Source: [Mora et al. 2004](#))

However, magnetite-based magnetoreception is not the whole story. Some birds and amphibians cannot orient properly in captivity unless they are exposed to short wavelengths of light, which suggests that the visual system may also play a crucial role in magnetoreception (e.g., [Wiltschko & Wiltschko 1981](#); [Deutschlander, Phillips, & Borland 1999](#)). This finding has led to the idea that magnetoreception might also be accomplished when a receptor molecule absorbs photons (light particles). The energy absorbed temporarily changes the chemical property of the molecule in a manner that makes it responsive to external magnetic fields ([Ritz, Adem, & Schulten 2000](#)). Photopigments known as cryptochromes are present in the retina of vertebrates; they possess such chemical properties and so are considered to be possible receptor molecules ([Gegear et al. 2010](#)). Recent work has focused on Cry4 as the most likely candidate cryptochrome involved in magnetoreception in birds ([Günther et al. 2018](#); [Pinzon-Rodriguez, Bensch, & Muheim 2018](#)).

We have seen how researchers have discovered the diverse set of sensory systems that animals use to acquire information from the environment. This information helps direct animals' behavior in the search for food, mates, and members of a social group. This is by no means a complete accounting of sensory capabilities, however: for instance, many species can acquire environmental information by detecting polarized light ([Horváth & Varjú 2004](#)). For now, it is important to realize that understanding how animals perceive their world provides greater insight into understanding their behavior.

So far, we have examined sensory systems of individual species. In the next section, we examine how adaptations in sensory systems evolve in response to selection pressures from other species.

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## 5.6 Predator and prey sensory systems coevolve

### Learning Objectives

After reading this section, you should be able to

- compare the contrasting selective forces on predators and their prey and
- explain the coevolutionary arms race in sensory systems involving bats and moths.

Interactions between two species can affect evolution when the fitness of each species is affected by the outcome of the interaction. For example, in a predator–prey encounter, successful prey capture enhances predator fitness, while prey that escape have higher fitness than those that do not. Selection will act on each species, but in opposite directions with respect to the interaction: it will favor predator adaptations that enhance capture efficiency while simultaneously favoring adaptations in prey that enhance escape. This common scenario can lead to what is often referred to as a **coevolutionary arms race** that in turn leads to changes in the traits of predators and their prey over time. Let's examine one such arms race that involves sensory systems.

### Insect tympanal organs: an evolved antipredator adaptation

As we discussed earlier, many insects have receptor organs that can detect sound frequencies ranging from 2 to 100 kHz. The basic structure, the tympanal organ, has a vibrating membrane called the tympanum, which is associated with an internal airspace. In addition, the tympanal organ has from one to several thousand receptors called chordotonal sensilla that transmit electrical impulses to the brain when stimulated by high-frequency sound waves. These structures are found on the thorax, legs, abdomen, or base of the wing, and they range from a single organ in praying mantises (Figure 5.26) to six pairs of organs in some grasshoppers (Yager 2012).

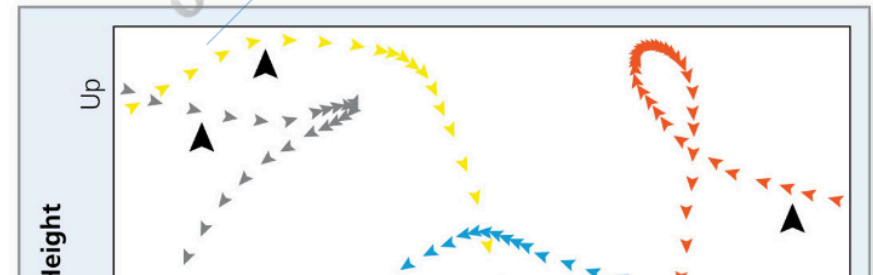


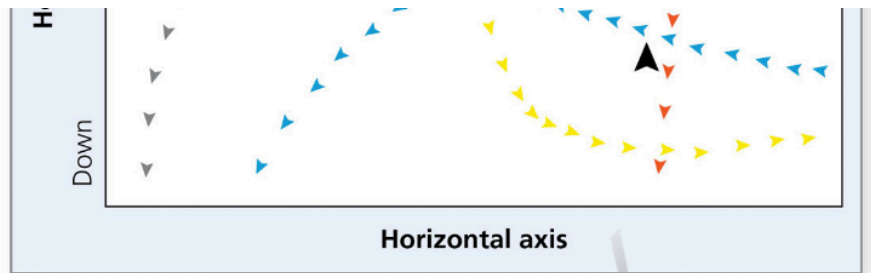
FIGURE 5.26. Tympanate ear. Praying mantis, showing the location of the tympanal ear opening.

Phylogenetic analyses suggest that ultrasonic-detecting insect organs evolved independently 18 different times. The presence of ultrasonic-detecting tympanal organs in so many diverse insect taxa may indicate that they evolved as an antipredatory response to their main predator, echolocating bats (Yack & Dawson 2008). Further support for this hypothesis comes from the fact that while insect species differ in the range of frequencies their chordotonal sensilla detect, most exhibit peak sensitivity between 20 and 60 kHz, the range of frequencies typically used by echolocating bats when they are hunting prey.

Echolocating bats vary the rate at which they emit ultrasonic vocal pulses. When bats search their environment, they produce pulses at a low rate ( $< 10$  pulses per second). When prey has been detected, they increase the pulse rate, presumably to facilitate orientation toward the moving object. Then, just prior to attack, they increase the pulse rate even more, to about 200 pulses per second as the attack is conducted. This variation in pulse rate provides important information to a potential victim that can detect it, regarding its distance from an approaching predator and the onset of an attack.

Once ultrasonic frequencies are detected, insects with tympanal organs display a variety of responses (Yager 2012). When low-pulse rate sounds are detected, individuals respond by flying away from the source, presumably to reduce probability of detection. However, when high-pulse rate sounds are detected, individuals exhibit rapid, erratic changes in their flight pattern and will often initiate a strong dive to avert capture (Figure 5.27). How effective are these antipredator behaviors?

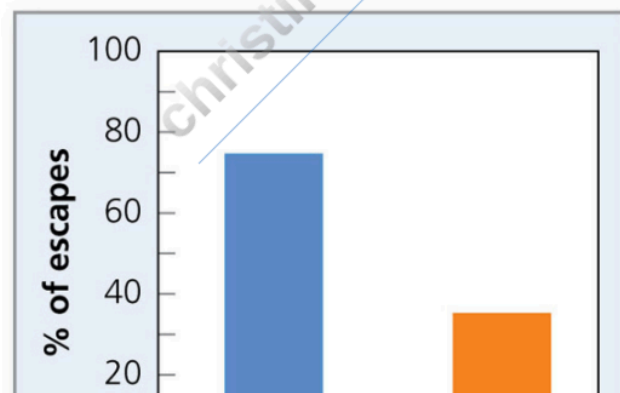




**FIGURE 5.27. Evasive flight in mantids.** Change in flight paths of four different mantids (different colors) after playing an ultrasonic click similar to one produced by a bat predator. The sequence of colored arrows represents the successive locations of a moth in two-dimensional space. Note that all individuals drop quickly (move lower on the y axis) after detecting the bat click (black arrows). (Source: [Yager 2012](#))

Jeffrey Tribblehorn and his colleagues tested the hypothesis that the ability to detect ultrasonic frequencies provides a strong survival advantage to species hunted by bats ([Tribblehorn et al. 2008](#)). The research team manipulated the ability of the praying mantis, *Parasphendale agrionia*, to detect ultrasound by filling their single tympanal organ with Vaseline. This method eliminated mantid responses to frequencies between 20 and 60 kHz, effectively deafening them to the ultrasonic frequencies used by hunting bats. The researchers examined bat–mantid interactions in free-flight encounters in a flight room. One mantid, either a control or a deafened individual, was released along with a single big brown bat (*Eptesicus fuscus*). The researchers recorded all bat vocalizations, the flight behavior of both individuals, and the outcome of the interaction (capture or escape).

Control mantids that could detect ultrasonic frequencies escaped in 74% of trials, typically by initiating a power dive just before the attack ([Figure 5.28](#)). In contrast, deafened mantids escaped in only 35% of trials, and none exhibited a power dive in response to an attack. These data support the hypothesis that the ability to detect ultrasonic frequencies is an effective antipredator adaptation. With this background, we now examine coevolution between bats and their prey.



**FIGURE 5.28. Percentage of mantid escapes.** Deafened mantids had a significantly lower escape frequency than individuals that could hear. (Source: [Tribblehorn et al. 2008](#))

## FEATURED RESEARCH Predator–prey sensory system coevolution in bats and moths

Nocturnal bats around the world have used echolocation to detect and pursue their prey for over 50 million years ([Figure 5.29](#)) ([Springer et al. 2001](#)). Predation using ultrasonic vocalizations created strong selection on their prey to detect an approaching bat, and an effective antipredator response evolved. Ears sensitive to ultrasonic bat vocalizations have evolved independently in six orders of insects: Lepidoptera (moths), Neuroptera (lacewings), Coleoptera (beetles), Mantodea (mantids), Orthoptera (crickets and grasshoppers), and Diptera (parasitic flies). As we saw in the previous section, this attribute allows individuals to take evasive action just prior to attack. But a second counteradaptation has also evolved in many species: the ability to produce ultrasonic sounds that can deter bat attacks. Two types of such adaptations are known to exist.



**FIGURE 5.29. Bat attacking a moth.** Bats use ultrasonic vocalizations to hunt moths.

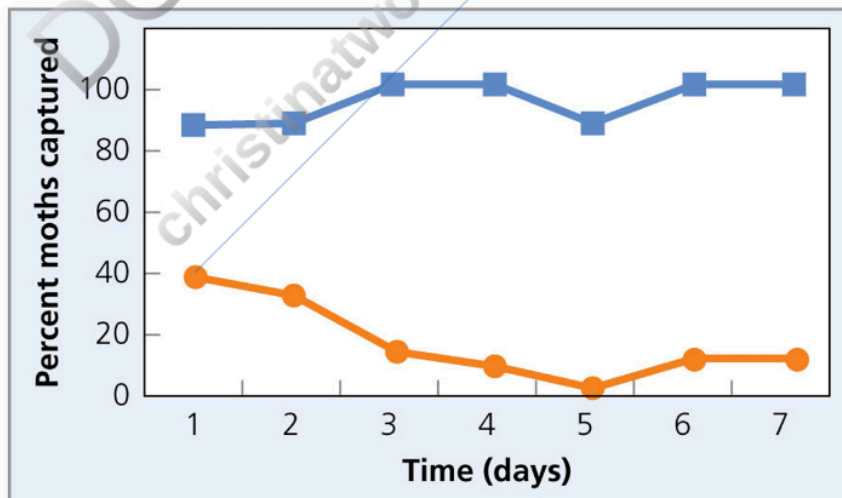


FIGURE 5.29. Bat attacking a moth. Bats use ultrasonic vocalizations to hunt moths.

The first is that some moths, particularly those in the family Arctiidae, contain toxic compounds that are distasteful to predators, including bats. Many species acquire these compounds from the plants they consume as caterpillars. In this large family, some species have evolved the ability to produce short, repetitive ultrasonic clicks using modified corrugated exoskeletal structures called tymbals. Bats can detect these clicks and learn to avoid the unpalatable species making them. The production of signals that indicate noxiousness is known as aposematism. (We will examine aposematism in more detail in [Chapter 6](#).) In a groundbreaking study, Dorothy Dunning obtained the first evidence of the antipredator nature of acoustic aposematism. She presented caged bats with unpalatable, ultrasound-producing arctiid moths and palatable, silent non-arctiid moths and found that the bats avoided the sound-producing moths more often than they avoided silent moths ([Dunning 1968](#)).

More recently, Nikolay Hristov and William Conner tested the acoustic aposematism hypothesis using naïve bats that had never been exposed to moth sounds ([Hristov and Conner 2005](#)). The hypothesis assumes that predators learn to avoid sound-producing moths because they are unpalatable. It predicts that bats will at first attack noxious, sound-producing moths but will quickly learn to associate the sound with bad taste and will attack sound-producing moths less frequently than they do silent moths.

Hristov and Conner tested the hypothesis by conducting a simple experiment in a flight cage in which they presented naïve big brown bats (*Eptesicus fuscus*) with moth species that differed in sound-production (S+ or S-) and chemical defense (C+ or C-) capabilities. Four moths of each type were offered as potential prey each day. When none of the moths were chemically defended, the bats attacked sound-producing and silent moths with a similar high frequency. However, when the sound-producing moths were noxious and the silent moths were palatable, bats very quickly learned to avoid the sound-producing moths, often after consuming just one of them ([Figure 5.30](#)). Thus, the ability to produce ultrasonic sounds, combined with a chemical defense, enhances the survivorship of arctiid moths that have evolved the ability to produce sounds that bats can detect.



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FIGURE 5.30. Percentage of moths captured as a function of moth traits. Naïve bats were put in flight cages with either a palatable, silent moth (blue) or a sound-producing, noxious moth (orange). Bats quickly learned to avoid noxious moths that produced ultrasonic clicks. (Source: [Hristov & Conner 2005](#))

The second hypothesized advantage of the production of ultrasonic sounds by arctiid moths is that it interferes with a bat's ability to echolocate by jamming the bat sonar. Many species of tiger moth in the genus *Bertholdia* produce complex acoustic sounds and increase the frequency of sound production just prior to a bat's attack. This suggests that the sounds might function to interfere with a bat's ability to localize and capture its prey.

Aaron Corcoran and his colleagues tested this hypothesis by examining interactions between big brown bats and one palatable species of tiger moth, *Bertholdia trigona* ([Corcoran, Barber, & Conner 2009](#)). They trained bats to attack tethered moths in a flight room. Moths were presented individually, and attack success was recorded. In treatment trials, a single *B. trigona* that was fully capable of producing sound was tethered in the room. Control trials included individual moths that were similar in size to *B. trigona* but were silent. In a second control, the researchers presented individual *B. trigona* that could not produce sounds because their sound-producing tymbals were ablated (removed).

Control moths (both silenced *B. trigona* and other silent species) were contacted over 400% more often than sound-producing tiger moths, and this difference in successful attack rate existed from the first trial and was constant over the course of the experiment. These data support the hypothesis that the ultrasonic sounds produced by palatable *B. trigona* are an effective antipredator adaptation that interferes with a bat's ability to successfully attack its flying prey.

In bat-moth predator-prey interactions, we see how differing fitness interests of species can lead to a coevolutionary arms race involving sensory system adaptations. Like all coevolutionary arms races, there is no ultimate winner: we expect ongoing evolutionary changes (novel adaptations) and counteradaptations in such species' interactions. For example, the European bat (*Barbastella barbastellus*) has evolved a novel counteradaptation: it produces ultrasonic pulses that are 10–100 times quieter than those produced by other aerial-hawking bats, which presumably makes it more difficult for moths to detect them ([Goerlitz et al. 2010](#)).

#### Video: Stealthy bats counter insect defenses

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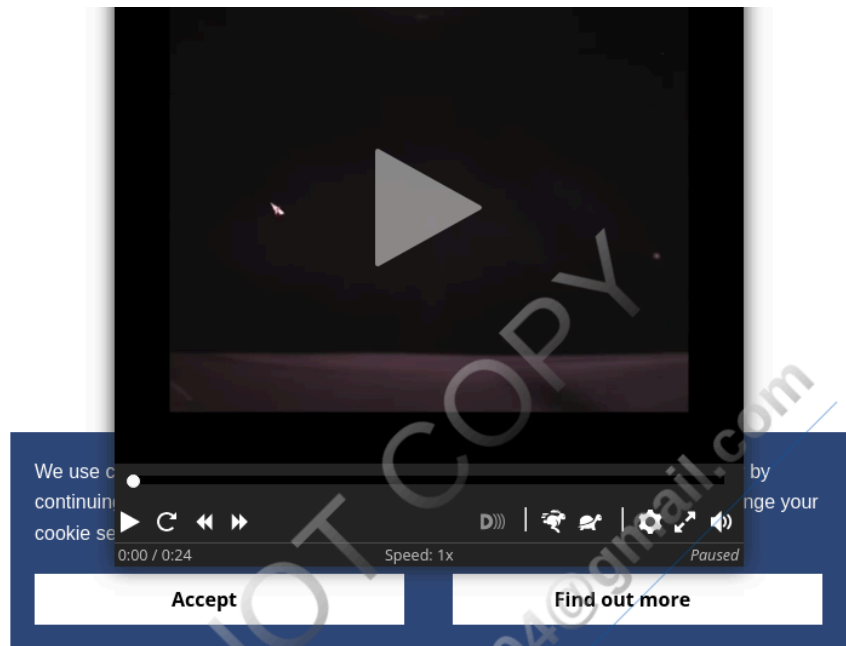
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**Video: Moth takes evasion action when detected and evades bat**

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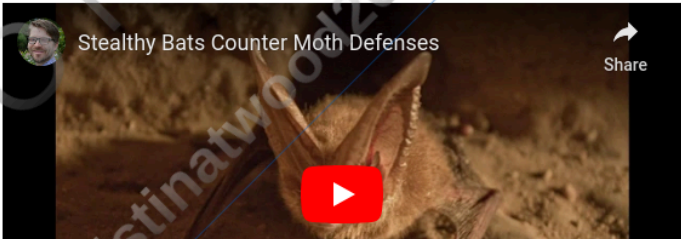
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## CHAPTER REVIEW

- 5.1 Animals acquire environmental information from their sensory systems**
- The umwelt is a species' perceptual environment.
  - The sensory system acquires environmental information.
- 5.2 Chemosensory systems detect chemicals that are perceived as tastes and odors**
- Multiple sensory receptors influence umami and sweet taste response in rodents.
  - Cuttlefish detect and respond to the odor of fresh conspecific eggs.
- 5.3 Photoreception allows animals to detect light and perceive objects as images**
- Behavioral assays reveal that monarch butterflies have true color vision.
  - Female pied flycatchers assess male UV reflectance in plumage to select a mate.
  - Crotaline snakes can detect and respond to warm objects.
- 5.4 Mechanoreceptors detect vibrations that travel through air, water, or substrates**
- Male ultrasonic pulses are an important component of mate choice by female moths.
  - Elephants use infrasounds to maintain contact among individuals in their group.
  - Nocturnal catfish find food by tracking the wake of their prey.
  - Antlions detect substrate-born vibrations made by their prey.
- 5.5 Some animals can detect electric or magnetic fields**
- Sharks can detect weak electric fields produced by their prey.
  - Many species can detect the Earth's magnetic field.
- 5.6 Predator and prey sensory systems**
- The sensory systems of bat predators

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# CHAPTER 4

## Behavioral Genetics

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Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 4.1 Behaviors vary in their heritability.
- 4.2 Behavioral variation is associated with genetic variation
- 4.3 The environment influences behavior via gene expression
- 4.4 Genomic approaches correlate gene expression with behavioral phenotypes
- 4.5 Genes can limit behavioral flexibility

### Features

- |                        |  |
|------------------------|--|
| Scientific Process     | 4.1 Environmental effects on zebrafish aggression  |
|                        | 4.2 Heritability of great tit exploratory behavior |
|                        | 4.3 Salamander personalities                       |
| Applying the Concepts  | 4.1 Dog behavior heritability                      |
| Toolbox                | 4.1 Molecular techniques                           |
| Quantitative Reasoning | 4.1 Aggressive personalities in sticklebacks       |

Our neighbor's Australian shepherd, Ryker, occasionally escapes from his yard to herd the sheep that live down the road. No one trained him to do this, but he displays herding behavior (Figure 4.1). Our own Labrador retrievers tirelessly retrieve balls, sticks, and toys and are adept in the water. Max and Grace race out each morning to combine retrieving balls with swimming in the pool (Figure 4.2). Dog breeds have a genetic predisposition to exhibit different behaviors—that is, their genes influence their behavior (Spady & Ostrander 2008). Over the past few centuries, Australian shepherds were bred for their herding behavior, while Labradors

were bred for retrieving. As we noted in Chapter 3, such distinctions are a result of the natural variation in early

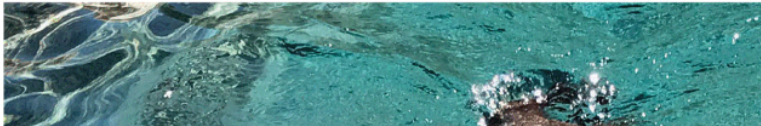
were bred for retrieving. As we noted in Chapter 3, such distinctions are a result of the natural variation in early dogs, which breeders could use to select dogs with the appropriate traits to breed (artificial selection). Individuals that performed well on specific tasks were selected for future breeding, and because these behaviors have a genetic component, they increased in frequency over time in each breed.



FIGURE 4.1. Herding behavior. Several breeds, such as this sheepdog, have been bred to herd livestock.

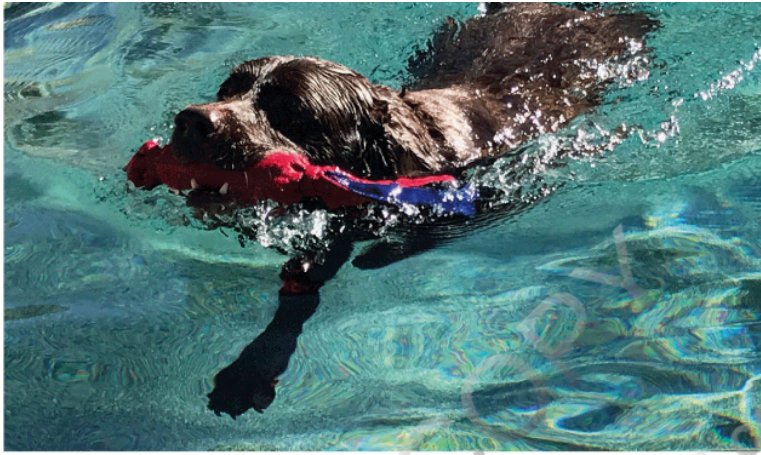
However, genes do not tell the whole story. The environment can also strongly affect animal behavior. For example, the early social environment of puppies can be a critical factor in their behavioral development. In fact, the Animal Medical Veterinary Association (AMVA 2015) recommends that puppies as young as eight weeks take socialization classes to minimize the risk of behavioral problems such as fear and aggression emerging in adulthood. In addition, although sheepdogs and retrievers naturally exhibit herding and retrieving behaviors, respectively, they need to be trained to fully develop these skills.

How, then, do genes and the environment affect animal behavior? Can we ascertain their relative importance in determining variation in behavior among individuals? In this chapter, we see how behavioral geneticists study the genetic and environmental influences on behavior that help to answer these questions. We begin by examining the heritability of behavioral traits.



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**FIGURE 4.2. Retrieving.** Retrievers were bred to retrieve game animals for hunters but, as this one demonstrates, will retrieve almost anything.

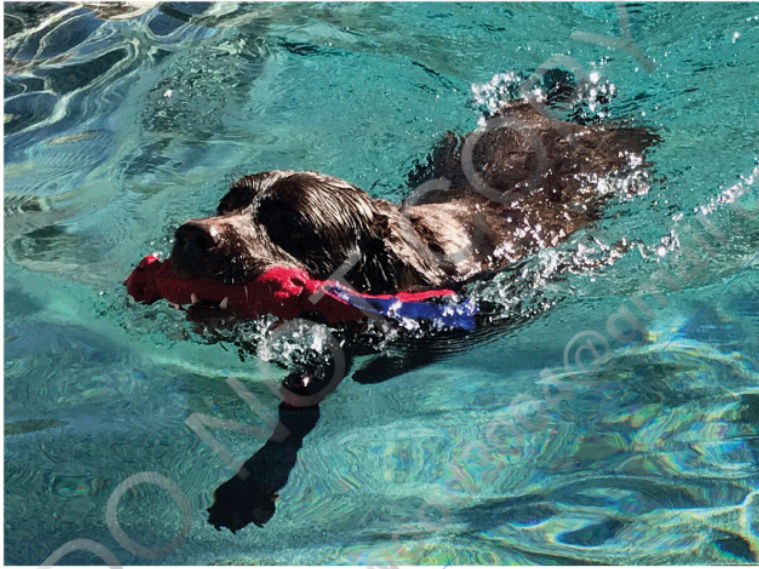
**Video: A sheepdog herding sheep**

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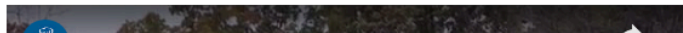
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## 4.1 Behaviors vary in their heritability

### Learning Objectives

After reading this section, you should be able to

- distinguish between phenotype and genotype,
- calculate  $H^2$  and  $h^2$ , and
- predict how a trait will respond to selection based on its heritability.

As we discussed in [Chapter 3](#), individuals within and across populations display natural variation in their phenotype, or their observable traits, such as behaviors and morphology. This variation is due to differences in their **genotypes** (genetic makeup) and their environment. Behavioral genetics examines how genes and the environment contribute to these differences in behavior by partitioning these effects.

An individual's behavior, or its behavioral phenotypic value ( $P$ ), is the result of three factors:

1. its genotype ( $G$ ) at all loci that affect the behavior;
2. the environment ( $E$ ) it has experienced; and
3. any interactions between them—more formally, gene–environment interactions ( $G \times E$ ).

Given that both genetic and environmental factors affect behavior, how can we assess their relative contributions?

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One way is to first break down the phenotypic variation of a population into its two components:

$$V_P = V_G + V_E$$

where  $V_P$  is the variation in the phenotype,  $V_G$  is the variation due to genetic effects, and  $V_E$  is the variation due to environmental effects. The last item includes all the environmental conditions that individuals experience, as well as their responses to those conditions.

We can now define the **heritability ( $H^2$ )** of a trait as the proportion of phenotypic variation in a population that is due to genetic influences:

$$H^2 = \frac{V_G}{V_P} = \frac{V_G}{(V_G + V_E)}$$

This proportion is known as *broad-sense heritability* because it includes all the genetic effects on the phenotype. Multiple genetic factors affect phenotypic variation, and they can be grouped into three types:

1. **additive effects (A)**, or the average effect of individual alleles on the phenotype;
2. **dominance effects (D)**, or the interaction between alleles at one locus, in which one allele can mask the expression (phenotype) of the other; and
3. **epistatic effects (epistasis, I)**, or the interaction between genes at different loci, such that one gene modifies the effect of another or acts with it to produce a new phenotype (Conner & Hartl 2004).

We can now define genetic variation as

$$V_G = V_A + V_D + V_I$$

Both dominance and epistatic effects involve interactions between alleles or genes and are therefore nonadditive. When chromosomes assort independently in meiosis, the effect of both dominance and epistasis on phenotypic variation is influenced by alleles present in individuals in each generation. Additive genetic variation effects, on the other hand, are independent of other genes or the environment. Thus, additive genetic variation is of primary importance for determining how a trait will respond to selection. The proportion of phenotypic variance that is due solely to additive genetic values is *narrow-sense heritability ( $h^2$ )*, which is the measure of heritability most commonly reported:

$$h^2 = \frac{V_A}{V_P}$$

Because each parent contributes a single allele per locus to offspring, the phenotypic similarity between offspring and parents depends on the additive effects of alleles. The greater the narrow-sense heritability of a trait, the more likely we are to observe a close resemblance between offspring and their parents in that trait. Therefore, narrow-sense heritability can be determined by examining the similarity of behavior between parents and their offspring.

As we saw in Chapter 3, heritability is commonly determined using parent-offspring regressions, in which the mean trait values of parents are regressed against the mean trait values of their offspring. The slope of the regression can range from zero to one: the higher the slope value, the more offspring resemble their parents. Higher slope values indicate that a greater proportion of the phenotypic variance is additive variance, or variation passed from parents to offspring. Lower slope values indicate that less of the phenotypic variance is due to additive genetic variance and is not transmitted to offspring. This means that more nonadditive and

Not surprisingly, a variety of narrow-sense heritability values have been reported for different behaviors. Lisa Meffert and her colleagues (2002) surveyed the literature and found that although there was a prevalence of low heritabilities for many behaviors, their conservative estimate of mean heritability from 73 studies was  $h^2 = 0.38$ . Examples of low values include those for oviposition behavior in weevils ( $h^2 = 0.05$ ) (Tanaka 2000) and vigilance in marmots ( $h^2 = 0.08$ ) (Blumstein et al. 2010). Examples of higher values include those for defense behavior in snakes ( $h^2 = 0.41$ ) (Garland 1994; Figure 4.3) and courtship behavior in crickets ( $h^2 = 0.72$ ) (Hedrick 1994).



**FIGURE 4.3. Garter snake defensive behavior.** Several defensive behaviors in garter snakes, like this open-mouth attack, have high heritabilities.

In the following sections, we examine the genetic and environmental influences on behavior, including their interaction. We begin with the genetic basis of behavior.

## APPLYING THE CONCEPTS 4.1

### Dog behavior heritability

In captive breeding programs, individuals are selected as parents for the next generation in order to pass on desired traits. Historically, breeders simply assumed that traits were heritable.

It is crucial, however, to know whether the trait has a heritable component because if behaviors are affected only by the environment, artificial selection will be ineffective.

A variety of behavioral tests have been developed to characterize the disposition or temperament of dogs (for a review, see Houpt 2007). For example, such tests are used to assess breeds that will be used as service dogs or in hunting. Individuals must demonstrate the



appropriate disposition for the situations they will encounter: service dogs must exhibit high levels of self-confidence (i.e., being nonreactive to novel situations) in a wide variety of environments, while hunting dogs must not react negatively (i.e., fearfully) to gunshots. Silvia Ruefenacht and colleagues used data from 25 years of standardized behavioral field tests on over 3,000 dogs with known pedigrees to determine the heritability of seven different behaviors in German shepherds (Ruefenacht et al. 2002), including self-confidence, reactions to different stimuli, reaction to gunfire, and play behavior. Heritability scores ranged from 0.09 to 0.24, with the highest score being reaction to gunshots. This finding confirms that, although selection for specific behavioral traits can be fruitful, the environment also exerts a great deal of influence on behavior. ■

## 4.2 Behavioral variation is associated with genetic variation

### Learning Objectives

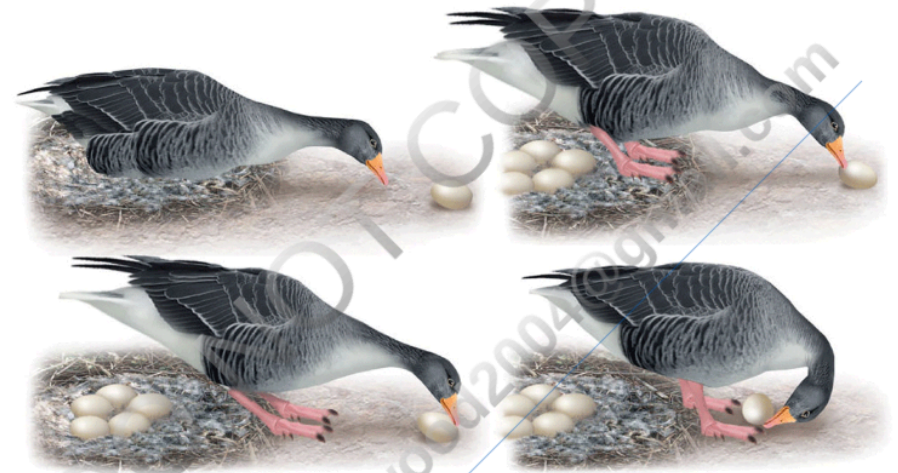
After reading this section, you should be able to

- explain how Bastock's fruit fly research demonstrated a link between genotype and phenotype,
- distinguish between major and minor genes, and
- differentiate between the functions of QTL mapping and knockout techniques.

Some of the earliest evidence for the genetic basis of behavior came from captive animals. Early researchers noted that many laboratory strains of mice and rats exhibited consistent differences in behavior (e.g., Yerkes 1913). Because individuals in captivity are usually reared in similar conditions, differences in behavior most likely result from differences in their genotypes (e.g., Plusquellec & Bouissou 2001; Augustsson & Meyerson 2004). Other evidence came from studies of instinct, or innate behaviors—behaviors that are performed the same way each time, are fully expressed the first time they are exhibited, and are present even in individuals raised in isolation. Because all individuals in a species exhibit innate, nonlearned behaviors, these behaviors must have a genetic basis, which also means that they are heritable.

Innate behavior includes reflexes, involuntary and often immediate behavioral responses to an external stimulus. One example is the blink reflex: the eyelid of many species, including humans, closes when an object moves quickly toward the eye. This reflex is common in vertebrates, as we learned firsthand when our dog Buck suffered facial nerve paralysis on his right side. The veterinarian confirmed the diagnosis by showing us that Buck's blink response was absent for his right eyelid but fully functioning for the left eyelid.

Examining innate behaviors, Konrad Lorenz and Niko Tinbergen noted that adult graylag geese (*Anser anser*), which lay their eggs in nests on the ground, will extend their neck and use their bill to gently roll displaced eggs back into the nest in a very fixed manner (Lorenz & Tinbergen 1957) (Figure 4.4). Tinbergen, a pioneer of modern animal behavior (see Chapter 1), also examined the innate escape response of newly hatched goslings (Tinbergen 1951). He noted that when a small shadow passed overhead, such as a predator silhouette, the chicks always responded by assuming a characteristic antipredator crouching position and looking up at the sky. In this case, the animals responded with a **fixed action pattern**—a behavior that displays almost no variation and, once started, is not stopped until completed. These observations led researchers to hypothesize that such behavior must be genetically based.



**FIGURE 4.4.** Graylag geese egg retrieval. Egg retrieval behavior is a fixed action pattern behavior initiated by the sight of an egg outside the nest. (Source: Lorenz & Tinbergen 1957)

### Video: Fixed action pattern in graylag goose

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Video: Fixed action pattern in graylag goose

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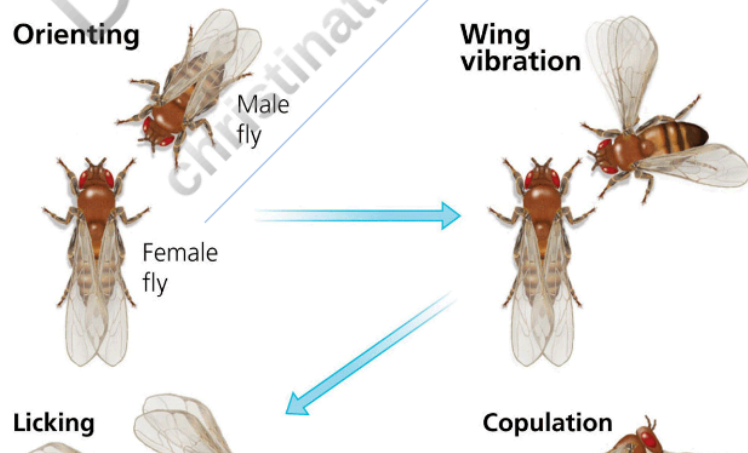
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## FEATURED RESEARCH Behavioral differences between wild-type and mutant-type fruit flies

More direct evidence of a genetic influence on behavior came from the work of John Paul Scott and Margaret Bastock, two researchers who each studied fruit flies (*Drosophila melanogaster*) (Scott 1943; Bastock 1956). In fact, Bastock, a graduate student of Tinbergen's, helped open the door to the new field of behavioral genetics.

In her dissertation, Bastock examined behavioral differences between a **wild type**, or the typical form in nature, and a mutant form of *D. melanogaster* called "yellow" because its body is yellow instead of the normal gray (Bastock 1956). This mutant form was rare in nature but arose frequently and reproduced successfully in laboratory stocks. Why aren't yellow forms more common in nature? Bastock wondered whether the gene mutation in yellow flies might induce a behavioral change that resulted in very low reproductive success in the wild. In other words, was genetic variation associated with behavioral variation?

Fruit fly courtship begins with the male orienting toward and then following the female. The male taps her with his foreleg, which has receptors—molecules on the surface of cells (or the nucleus) that receive chemical information—that identify sex and species. Next, the male begins a wing vibration, a form of courtship song, which is followed by the male licking the female. If she is receptive, they copulate (Figure 4.5).



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**FIGURE 4.5. Fly courtship.** Male fruit fly courtship behavior follows a sequence of events that includes orienting toward the female, vibrating the wings (song production), and licking the female genitalia, which can lead to copulation. (Source: Sokolowski 2001)

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(Caillaud & Via 2012). Pea aphids (Figure 4.9) have sucking mouthparts, called stylets, which they use to pierce the soft tissues of plants, such as leaves or stems, to feed on the sap in the phloem. In a population in New York, Caillaud and Via identified two genetically distinct races of pea aphids that feed on different plant species: one specializes on alfalfa and the other on clover. How do individuals select the correct plant species for feeding? Aphids explore the plant surface and subepidermic tissues, probe deeply to find phloem sap, and evaluate it prior to ingestion (Caillaud & Via 2000). The duration of these behaviors will differ greatly depending on whether an aphid is on a preferred or nonpreferred plant species.



**FIGURE 4.9. Pea aphid feeding.** Pea aphids feed on plants by extracting sap.

For the QTL analysis, the researchers created F1 and F2 generations that resulted from crossing individuals of the two races. Next, they characterized the behavioral phenotype of plant choice behavior for individuals from the F1 and F2 generations, as well as that for each parental race. They then measured total time spent actively searching and probing tissue for a feeding site, time spent immobile or walking while not penetrating plant tissue, the latency to inject saliva into the plant to begin the digestive process, and the amount of time spent digesting sap from each plant. A strong plant preference was indicated by a rapid time to feed. They assessed the genotype of each individual using 116 amplified fragment-length polymorphism markers (Vos et al. 1995). In this technique, genomic DNA is cut into pieces, or fragments. Known genetic markers (pieces of DNA) are then attached to each piece to create a linkage map showing the position of markers relative to each other, but not their specific location on the chromosome.

Caillaud and Via found from one to three QTLs for the total time spent searching for a feeding site, the time spent on a plant before penetrating it, and the time spent digesting sap from each plant. The proportion of the behavioral variation in plant acceptance behavior explained by each QTL ranged from 7% to over 50%. Given the small

number of QTLs and the large proportion of variance for which they accounted, the researchers proposed that perhaps only a few genes are involved with plant selection behavior. They did not find any QTL for latency to inject saliva into the plant, which probably indicates that this particular behavior is influenced by numerous minor genes.

All of these examples illustrate how researchers have identified genetic influences on behavior. We've seen that researchers use both indirect (e.g., the studies on fruit flies and fire ants) and more direct methods (e.g., knockout studies) to examine the relationship between genotypic and behavioral variation. But recall that genes are just one factor that influences behavior; the environment also plays a role.

## 4.3 The environment influences behavior via gene expression

### Learning Objectives

After reading this section, you should be able to

- explain how to study environmental influences on behavior,
- describe how microarray analysis and knockdown techniques are used to study environmental influences on gene expression and behavior, and
- explain why gene-environment interactions generate enhanced population variation in phenotypic traits.

Variation in the environments that individuals experience can result in behavioral variation among individuals. Recall that genes do not produce specific behaviors but rather code for a diverse array of molecules that affect brain function and thus behavior, a process known as **gene expression**. Animals acquire sensory inputs about both the abiotic and biotic aspects of the environment, including the presence of others, such as conspecifics or predators. These inputs are integrated in the brain and can result in differential gene expression. In other words, genes and their products are expressed at different times and in different environmental conditions, depending on sensory inputs.

One approach used to identify environmental effects on behavior is to expose closely related individuals to different environments. If such individuals (with similar genes) exhibit different behaviors, they are likely the result of environmental factors.

### FEATURED RESEARCH Environmental effects on zebrafish aggression



Christopher Marks and colleagues examined how water conditions during development affect aggressive behavior in adult zebrafish (*Danio rerio*) (Marks et al. 2005) (Scientific Process 4.1). Zebrafish live in a variety of habitats throughout the Himalayas, ranging from oxygen-rich fast-flowing streams to oxygen-poor stagnant pools. Oxygen depletion, or hypoxia, is a common stress for aquatic organisms that can affect their development and behavior. Marks and colleagues raised closely related zebrafish in water that had either low or high oxygen levels (hypoxic and normoxic environments, respectively) and then examined aggressive behavior in adults when placed in each type of environment. This design allowed the researchers to determine the effect of different environmental conditions on zebrafish behavior: the developmental environment (DE) and the behavioral test environment (TE).

#### SCIENTIFIC PROCESS 4.1

##### Environmental effects on zebrafish aggression



Research Question: How does environmental variation affect aggression in zebrafish?

##### Hypothesis:

Both developmental environment (DE) and behavioral (test) environment (TE) affect aggression.

##### Prediction:

(a) If only DE affects behavior, aggression will be unaffected by TE and will be highest in normoxic (high-oxygen) water. (b) If both DE and TE affect behavior separately, aggression will

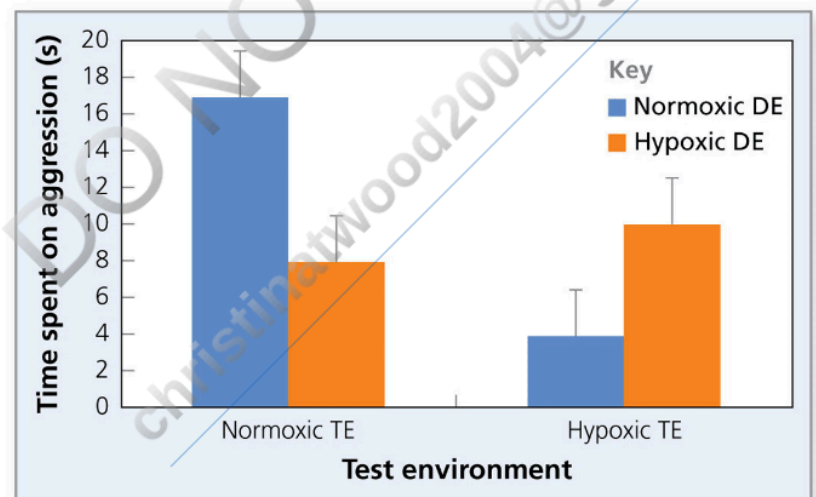
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normoxic (high-oxygen) water. (c) If both DE and TE affect behavior separately, aggression will be higher for fish in a normoxic TE and will be highest for fish whose DE was normoxic. (d) If DE and TE interact, aggression will be highest for fish whose TE and DE match.

##### Methods:

The researchers:

- Collected eggs from 12 full-sibling clutches (all individuals shared 50% of gene alleles because members of a clutch have the same parents)
- Divided the eggs into two developmental environments (normoxic and hypoxic). The embryos were raised until adulthood (about 75 days old) with unlimited food. Normoxic development treatment tanks had continuously oxygenated water (high dissolved oxygen content = 6.8 mg/L); hypoxic development treatment tanks had nitrogen gas bubbled into the water (low dissolved oxygen content = 0.8 mg/L)
- Tested fish in either a normoxic or a hypoxic test chamber after a 16-hour acclimation period
- Measured aggression as time spent biting or nipping a mirror image



**FIGURE 1. Results.** The blue bar represents the normoxic and the orange bar the hypoxic development environment. (Source: Marks et al. 2005)

##### Results:

Hypoxia raised fish had higher levels of aggression in the hypoxic test chamber, and normoxia

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Hypoxia-raised fish had higher levels of aggression in the hypoxic test chamber, and normoxia-raised fish had higher levels of aggression in the normoxic test chamber.

#### Conclusion:

Zebrafish display more aggressive behavior in the environment in which they were raised, indicating an interaction between developmental and behavioral environments.

#### Evaluate

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Explain why the researchers used full siblings in their experiments.

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After the fish had matured, they were tested for aggressive behavior in one of the two environments. Aggression assays were conducted by placing a small mirror on one wall of the test chamber. Fish respond aggressively to their mirror image because they treat it as they would an intruder. The researchers videotaped the behavior of each

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fish for two minutes after the mirror was installed and recorded the amount of time the fish spent butting or nipping the mirror.

Within the normoxic test environment, fish raised in the normoxic developmental environment were more aggressive than fish reared in the hypoxic developmental environment. Similarly, in the hypoxic test environment, fish raised in the hypoxic developmental environment exhibited higher levels of aggression than fish reared in the normoxic developmental environment. In both cases, then, individuals displayed higher levels of aggression when the developmental environment and test environment were the same.

Because the experimental design used full siblings reared in different environments, the results demonstrate how the environment can affect behavioral phenotype. Marks and colleagues suggested that aggressive behavior is energetically costly and that this cost may become particularly high when fish experience a novel oxygen environment. Fish reared in normoxic environments probably experience an oxygen deficiency when in hypoxic conditions and so are incapable of high levels of activity. It is less clear why fish reared in hypoxic environments exhibited slightly lower levels of aggression in normoxic conditions; further research on this phenomenon is needed.

This study demonstrates how variation in the abiotic environment can result in variation in behavior. In the next section, we discuss a common proximate mechanism that explains how the environment influences behavior.

## FEATURED RESEARCH Social environment and gene expression in fruit flies

Studies examining environmental influences on behavior often characterize gene expression of individuals exposed to different environments. A common approach manipulates social environment, which can refer to the presence, type, and number of nearby individuals, as well as interactions with such individuals. Why might differences in the social environment affect behavior? Consider that behavioral interactions between two conspecifics often depend on the sex of the participants: male–male interactions may involve aggressive behaviors, while male–female interactions often involve courtship behaviors. Lisa Ellis and Ginger Carney used microarray analysis ([Toolbox 4.1](#)) to examine gene expression in male fruit flies exposed to different social environments ([Ellis & Carney 2011](#)). In particular, they wanted to determine how the social environment of individuals affects gene expression. Is there differential gene expression for male–female interactions than for male–male interactions or a set of “socially responsive” genes that are expressed in all social interactions?

Ellis and Carney raised male flies and exposed them to one of two treatment groups or controls. One treatment group was allowed to court a single female, while the other interacted with a rival male, both for 20 minutes. Control males did not interact with any other fly. Microarray analysis was performed, using DNA from the heads of flies in these two groups, to examine differences in gene expression in the brain and important sensory organs such as the antennae.

The researchers identified hundreds of genes that were socially responsive. Of these, 505 responded to male–male interactions and 281 responded to male–female interactions. However, many of these genes were expressed in both treatments and so are presumed to be socially responsive genes involved in all conspecific interactions. The analysis also identified 240 genes that were responsive only to the male–male interaction treatment but only 16 genes uniquely responsive to male–female interaction. Thus, the researchers identified 16 candidate genes

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genes uniquely responsive to male–female interaction. Thus, the researchers identified 16 candidate genes associated only with male courtship behavior, while hundreds of other genes were determined to be involved in male–male interactions. Why there is such a difference in the number of genes involved in these different social interactions is unclear, but environmental conditions clearly affect gene expression, and its resulting behavior, in male fruit flies.

## Social environment and birdsong development

A second area of much work on how environmental effects influence behavior examines birdsong. All birds produce simple vocalizations, known as calls, which are innate. Many birds, particularly songbirds in the suborder Passeri (of the order Passeriformes), also produce complex vocalizations known as songs, which are used to defend a territory and attract a mate. Birds use their syrinx to produce vocal sounds, and in many songbird species, only males sing (although in tropical species, often both sexes sing).

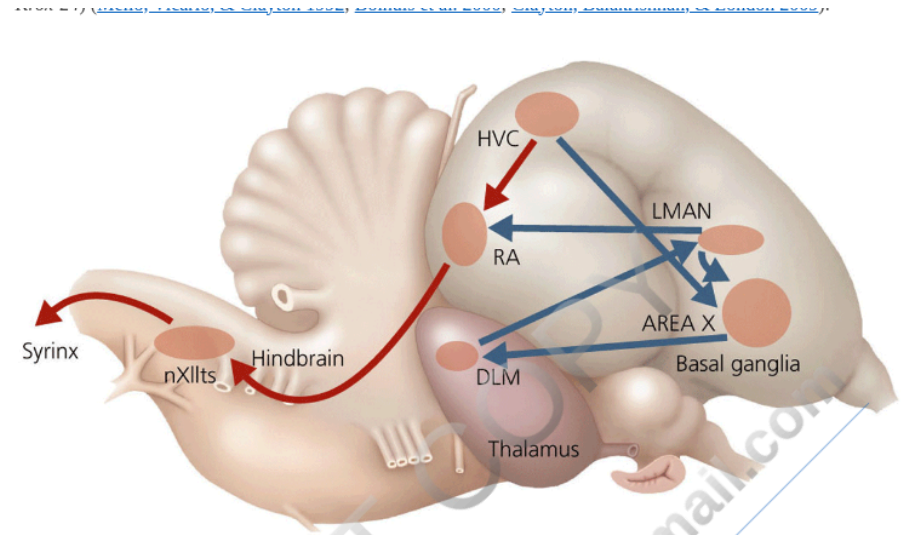
Environmental exposure to conspecific song is a critical factor for proper song development in birds (e.g., [Beecher & Brenowitz 2005](#)). Song learning occurs in several stages, and species are classified as closed- or open-ended learners. Closed-ended learners must hear a tutor sing its conspecific song shortly after hatching. During this sensitive period, which may last for several weeks, the bird apparently learns the song but does not attempt to reproduce it. When singing begins, birds produce vocalizations known as a subsong, which initially differs greatly from, but then converges to, the song learned from the tutor. Finally, a bird's song becomes crystallized and does not change. In contrast, a fixed sensitive period does not exist for open-ended learners, which can acquire new song elements throughout life.

Early work on song learning in closed-ended learners relied on socially isolated birds hearing a taped tutor. This approach maximized control of the learning environment and showed that birds deprived of a tutor failed to develop proper song (e.g., [Marler & Peters 1977](#)). Subsequent work revealed that song learning is affected by the type of tutor. For white-crowned sparrows (*Zonotrichia leucophrys*), the sensitive period lasts longer when a subject is paired with a live tutor rather than a taped tutor ([Baptista & Petrinovich 1984](#)). In addition, while the songs of live-tutored birds largely matched those of wild birds, tape-tutored birds produced much simpler songs, with a repertoire only about half the size of that of wild birds ([Chaiken, Böhner, & Marler 1993](#)). These results fostered better understanding of the role of environmental influences on song learning (e.g., [Beecher et al. 2007](#)). The next step was to understand the neural physiology and genetics of song learning, as we see next.

## FEATURED RESEARCH Social environment and gene expression in birds

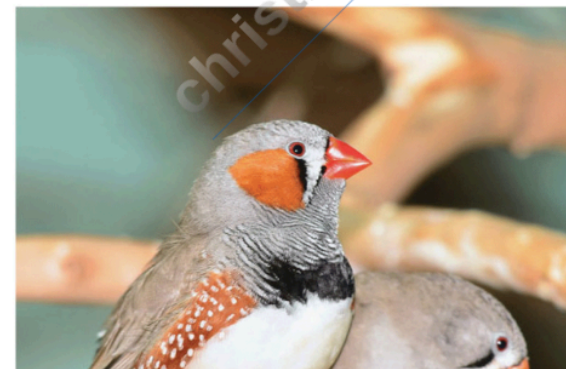
The brains of songbirds differ greatly from those of non-songbirds, with the former having enlarged and interconnected areas involved in song memory and production. These areas of the brain, called the song system, consist of a posterior nucleus, which controls sound production (airflow and the syrinx), and an anterior nucleus involved in song learning. An important localized region in the anterior nucleus is Area X ([Figure 4.10](#)). Exposure to birdsong, particularly conspecific song, causes numerous genes to be expressed in different regions of the song system. The most important appear to be *FoxP2* and *ZENK* (an acronym for the genes *zif-268*, *Erg-1*, *NGFI-A*, and *Krox-24*) ([Mello, Vicario, & Clayton 1992](#); [Bolhuis et al. 2000](#); [Clayton, Balakrishnan, & London 2009](#)).

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**FIGURE 4.10. Avian song circuit.** There are two neural circuits in the songbird brain. The red arrows indicate neural connections within the posterior circuit, which is involved in song production. The blue arrows indicate connections in the anterior circuit, which is involved in song learning. HVC = neostriatal nucleus; RA = robust nucleus of the arcopallium; DLM = medial nucleus of the dorsolateral thalamus; LMAN = anterior neostriatum; nXllts = tracheosyringeal neuron. (Source: [Clayton, Balakrishnan, & London 2009](#))

One way these genes were identified was by impairing their function and observing the effects on song development. Sebastian Haesler and colleagues used this approach to determine the role of *FoxP2*, which encodes the forkhead box protein P2, in zebra finches (*Taeniopygia guttata*) ([Figure 4.11](#)) ([Haesler et al. 2004](#)). They found that *FoxP2* undergoes increased gene expression in Area X of a bird's brain both when young birds learn to sing and when open-ended learning adults change their song. This result suggests that *FoxP2* plays a role in song learning.



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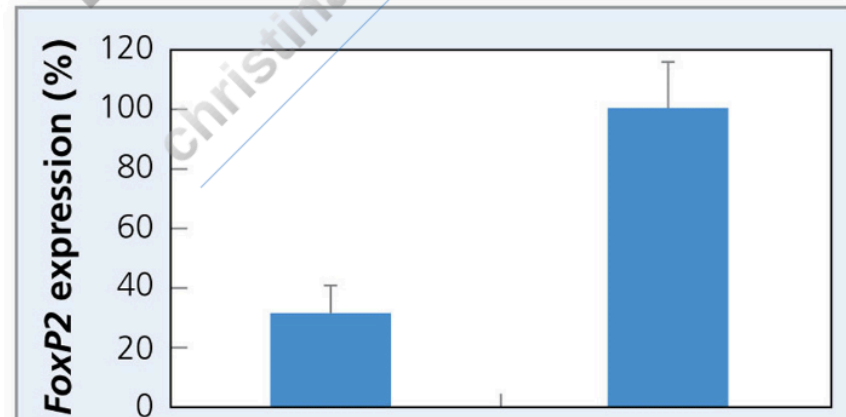




**FIGURE 4.11. Zebra finch.** Zebra finches learn their songs from tutors.

Haesler's research team then reduced *FoxP2* levels in Area X before young zebra finches began to learn their song (Haesler et al. 2007). They used a knockdown technique, which involved using a virus to insert short sections of RNA into the *FoxP2* gene at two different locations to reduce its expression (a knockout technique had not yet been developed for songbirds). Control birds had a short section of RNA inserted into a noncoding region of DNA that had no effect on the gene's expression. Each subject was kept in a sound-isolation chamber with an adult male tutor during the critical period when young finches learn a tutor's songs. At this time, the songs of both the tutor and the subject were recorded. To quantify the similarity of acoustic elements between the vocalizations of two individuals such as subject and tutor (e.g., Nordby, Campbell, & Beecher 2001), the researchers used spectrograms, or sonograms: two-dimensional representations of sound that allow researchers to characterize the acoustic structure of vocalizations. Spectrograms can reveal the number of song elements and their characteristic features (e.g., maximum frequency, maximum duration, and intervals between elements).

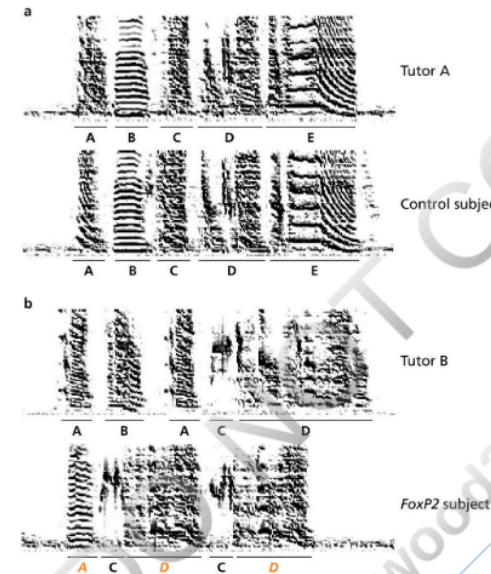
In knockdown birds, *FoxP2* expression was reduced by approximately 70% (Figure 4.12), which affected their song development: acoustic similarity between the tutor and the knockdown subject was much lower than it was in the controls. Knockdown birds tended to omit specific syllables and failed to copy accurately the duration of some song syllables (Figure 4.13). Because birds with experimentally reduced gene expression of the *FoxP2* gene in Area X inaccurately learned their tutor song, the researchers concluded that *FoxP2* is required for normal song development.



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**FIGURE 4.12. *FoxP2* expression.** Mean (+ SE) *FoxP2* expression in knockdown and control birds. The expression of the *FoxP2* gene in Area X of the brain was significantly lower in knockdown birds compared to controls. (Source: Haesler et al. 2007)



**FIGURE 4.13. *FoxP2* knockdown spectrograms.** (a) The spectrograms of a control tutor song (top) and subject song display a high degree of song matching. (b) The spectrograms of *FoxP2* knockdown subjects do not match those of their tutor (top) well. Letters indicate different song elements. (Source: Haesler et al. 2007)

These examples illustrate how researchers investigate environmental influences on behavior. They also demonstrate how variation in environments can enhance behavioral variation in a population. In the next section, we examine how genetic and environmental conditions can interact to produce even greater phenotype variation in populations.

#### Video: Zebra finch song and sonogram

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## Gene–environment interactions

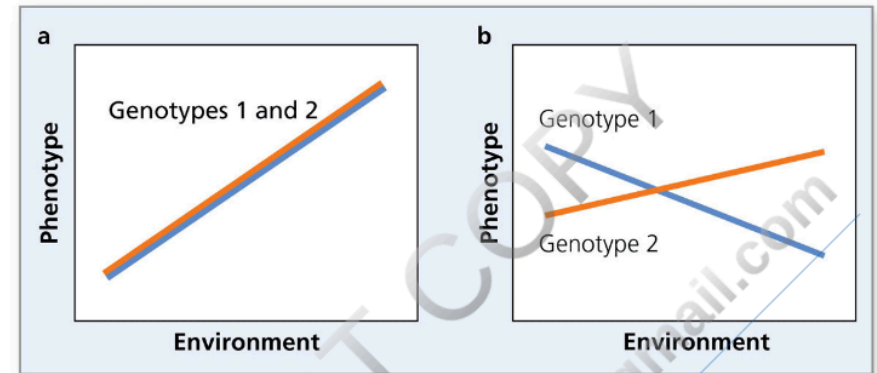
As we have seen, both genes and the environment can significantly affect variation in behavioral phenotypes. How might these factors interact to affect behavioral phenotypes? Suppose you raised two populations of genetically identical aphids, a single genotype, in different environments (say, on different plants) and observed some aspect of their feeding behavior. The range of different behavioral phenotypes observed from the single genotype raised across different environmental conditions is known as the reaction norm. This difference in phenotypes, phenotypic plasticity, indicates that the trait is not fixed but can respond to variation in the environment, just as we saw for zebrafish aggression.

Now consider a comparison of the reaction norms of different genotypes. One might expect that each genotype would exhibit a similar response to the different environments (Figure 4.14a). However, genotypes may respond very differently; when this occurs we say there is a significant gene–environment interaction ( $G \times E$ ) (Figure 4.14b). Where gene–environment interactions exist, we observe variation among genotypes in their responses to

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environmental variation. In this case, phenotypic variation in a population ( $V_P$ ) is enhanced and now results from three factors: variation in genotypes ( $V_G$ ), variation in environments ( $V_E$ ), and variation that results from their interaction ( $V_{G \times E}$ ). That is,

$$V_P = V_G + V_E + V_{G \times E}$$



**FIGURE 4.14. Environmentally influenced phenotypes.** Genotypes often exhibit variation in phenotype when exposed to different environments, illustrating a reaction norm. (a) Each genotype exhibits the same reaction norm. (b) The two genotypes exhibit different reaction norms because they respond differently to variation in the environment, evidence of a  $G \times E$  interaction.

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involves using closely related individuals reared in different environments to examine environmental influences on behavior. Another examines how variation in social environments leads to differential gene expression. This type of study has revealed potential candidate genes involved in social behaviors of flies and in song learning among birds. Finally, we have seen how gene–environment interactions are revealed in studies of flies; articulating these interactions allows researchers to better understand genetic and environmental influences on behavior. Studies of genetic and environmental variations, and their effects on behavior, will continue to inform our understanding of behavioral variation in animals. Next we examine recent advances in molecular biology that focus on examining the whole genome to further characterize how gene expression is associated with behavior.

#### Video: Foraging assay for rovers and sitters

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## 4.4 Genomic approaches correlate gene expression with behavioral phenotypes

### Learning Objectives

After reading this section, you should be able to

- describe the type of data genomic approaches generate and
- explain how a genomic approach informs our understanding of different behavioral phenotypes.

Advances in molecular biology, particularly the development of new genetic approaches, have allowed unprecedented understanding of the links between the genome and phenotype. **Genomics** or genomic approaches are genome-wide association studies that focus on entire genomes or large numbers of genes and often examine gene expression. Genes are expressed in a process in which DNA is transcribed into mRNA, which is translated into a sequence of amino acids. Many genomic studies use a technique called RNAseq where they can sequence and quantify the transcription of all transcripts (mRNA) in specific tissues. They then measure differentially expressed genes from individuals that exhibit different behaviors or that experience different environmental conditions. Measuring differential gene expression allows researchers to address proximate questions of behavior involving developmental, neurological, or immunological processes, along with ultimate questions involving behavioral evolution. Here, we will examine two studies to see how researchers use genomic approaches to better understand the proximate links between the genome and behavior.

### FEATURED RESEARCH Scouting behavior in bees

A focal organism for much genomic work in behavior is the honeybee, *Apis mellifera*, because its entire genome has been sequenced. Honeybees live in large colonies and adults exhibit marked differences in behavior. Up to 25% of the individuals in a colony act as food scouts, searching independently for new food sources. Non-scout individuals never embark on such searches but learn about the location of a new food source when, for instance, scouts perform a dance behavior. Thus scouts exhibit novelty-seeking behavior while non-scouts do not.

Zhengzheng Sophia Liang and her colleagues investigated the genomics of novelty-seeking behavior by focusing on food scouting behavior (Liang et al. 2012). The research team identified food scouts through feeding experiments in a large outdoor flight cage. All individuals were first trained to obtain food from a single available source, a training feeder with unscented sugar syrup and a yellow-colored floral pattern. Every bee that visited the feeder was marked with a spot of paint on the thorax. After three days, a second food source with a novel odor and visual pattern was added at a new location within the flight cage. Some bees found the new food source (scouts) and used it while others did not (non-scouts). All bees that visited the novel feeder were paint-marked, collected, and held until the end of the day to prevent them from recruiting other bees. After three days, the additional food source was replaced with another food source in a different location and with a different odor and visual pattern. The researchers repeated this procedure several times. They identified scouts as bees that found at least two or more of the new food sources, which reduced the likelihood of accidental discovery (finding just one novel feeder) and misidentifying a scout.

The research team dissected whole brain tissue from 20 scouts and 20 non-scouts and conducted a whole-genome



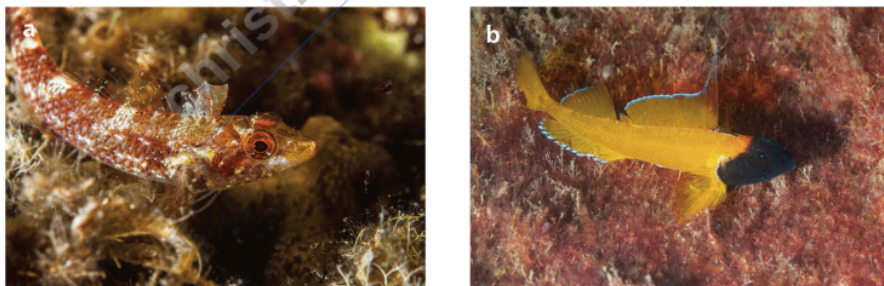
The research team dissected whole brain tissue from 20 scouts and 20 non-scouts and conducted a whole-genome RNA analysis. Sixteen percent of the mRNA transcripts, RNA copies of a gene, exhibited significant differences between scout and non-scout brains. Many of the differentially transcribed genes were related to neurotransmitter signaling involving catecholamine, glutamate, and gamma-aminobutyric acid (GABA), which are also known to influence novelty-seeking behavior in vertebrates.

This genome analysis shows that gene products in novelty-seeking individuals differ from those of bees that do not search for new food sources. Liang and colleagues found differential gene expression for several neurotransmitters, thereby providing important information about genes that influence such behavior. What is not yet known is how these neurotransmitter systems interact. Two of them are found in a part of the insect brain involved in reward learning, but other brain regions may be involved as well.

## Genomics and alternative mating tactics in fish

Learning to find food is one important adaptive behavior; reproducing is another. In many species, dominant, aggressive males defend a territory where they attract and mate with females. But defending a territory is costly because “territorial” males must chase away rival intruder males, which limits time available for feeding. Therefore not all males are able to defend a territory successfully. As mentioned in [Chapter 3](#), subordinate males often adopt a different behavioral strategy to reproduce: they sneak into a dominant male’s territory during mating and fertilize a female’s eggs. These “sneaker” males tend to be smaller than territorial males and often behave and look like females.

Are the behavioral and morphological differences among territorial and sneaker males correlated with different levels of gene expression? Celia Schunter and her colleagues examined this question in black-faced blennies (*Tripterygion delaisi*) ([Schunter, Vollmer, Macpherson, & Pascal 2014](#)). In the non-reproductive season all adult males and females have a dull, camouflaged body coloration. However, during the three-month reproductive period, some males rapidly develop a black head and bright yellow body and defend territories where they attract females to lay eggs that they fertilize ([Figure 4.20](#)). Males that do not change color exhibit a sneaking tactic to reproduce. The color change exhibited by territorial males is transitory and is only observed during the reproductive season, but all males are physiologically capable of developing territorial color and behavior.



**FIGURE 4.20.** Coloration differences in black-faced blennies, *Tripterygion delaisi*. a) Dull camouflaged body coloration and b) territorial male coloration of black-faced blennies.

Because the genome for this species has not yet been sequenced, the research team had to perform de novo assembly from small fragments of RNA sequence reads. Using this method, they examined whole-genome gene expression differences between the three phenotypes present during the reproductive period: territorial males, sneaker males, and females. When comparing these phenotypes, they found that territorial males differentially expressed more genes than sneaker males and females. Thus, maintaining the territorial morphology and behavior may require more genes to be expressed. When comparing males and females, the researchers found a greater difference in gene expression between the two male phenotypes than between males and females. This could indicate that male phenotypic plasticity, the ability to change behavior and morphology during the reproductive season, is more strongly associated with differential gene expression than sexual dimorphism. The territorial males expressed some genes related to synaptic plasticity, while the sneaker males differentially expressed genes associated with differentiation and development. Interestingly, the genes expressed for the male mating tactics appear to be species specific, as they are novel and distinct from previously suggested candidate genes in other species with similar behaviors.

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## 4.5 Genes can limit behavioral flexibility

### Learning Objectives

After reading this section, you should be able to

- identify an example of an animal personality trait,
- design two types of experiments to determine if a personality trait is heritable,
- explain how theoretical models show how different animal personalities can coexist in a population, and
- describe how the environment can influence the development of animal personalities.

So far we have seen how genetic factors, environmental factors, and their interaction produce variation in behavior. Genes also appear to limit behavioral variation. We all have met people who are consistently shy, as well as others who are consistently outgoing. Animals, too, display **personalities**—consistent differences in behavior over time or across different environmental contexts. Animal personality traits include variations in boldness (the willingness to take risks and explore novel objects), overall level of activity, and aggressiveness (Sih, Bell, & Johnson 2004; Stamps & Groothuis 2010). Are such traits heritable?

Niels Dingemanse and his colleagues examined the heritability of exploratory behavior in free-living great tits (*Parus major*) (Dingemanse et al. 2002). The great tit is a small, colorful passerine bird found throughout much of Europe and Asia. It is a common inhabitant of woodlands, parks, and gardens, where it feeds on insects and seeds. It nests in tree cavities as well as nest boxes. Because of its widespread distribution, abundance, and use of artificial nesting sites, the great tit has become a favorite study subject for behaviorists.

Previous work indicated that individuals exhibit consistent differences in their exploratory behavior, indicative of personalities, when placed in novel environments: some actively explore their new environment quickly (bold individuals), while others are more reticent and slower to explore (shy individuals) (Verbeek, Drent, & Wiepkema

1994; Drent & Marchetti 1999). Dingemanse and colleagues used birds from two populations in the Netherlands as part of a long-term research project. The birds bred in artificial nest boxes, which made it easier to capture them and determine relatedness (e.g., mother–offspring relationships). Birds were captured at the nest, uniquely color-banded, and, as adults, placed in an aviary that contained five novel artificial wooden “trees.” The research team recorded the number of flights and hops that birds took in the aviary in the first two minutes as an index of exploratory behavior. Individuals were then released back into the wild (Scientific Process 4.2). The team found a significant positive correlation between a mother’s exploratory score and that of her offspring, demonstrating heritable differences among individuals in this behavior.

### SCIENTIFIC PROCESS 4.2

Heritability of great tit exploratory behavior



Research Question: *Is exploratory behavior in great tits a heritable trait?*

#### Hypothesis:

Exploratory behavior has a genetic component.

#### Prediction:

There will be a positive correlation between a parent’s exploratory behavior and that of its offspring.

#### Methods:

The researchers:

- Placed individuals in an aviary (4.0 m × 2.4 m × 2.3 m) that contained five artificial wooden trees
- Recorded the number of flights and hops in the aviary in the first two minutes as an index of exploratory behavior

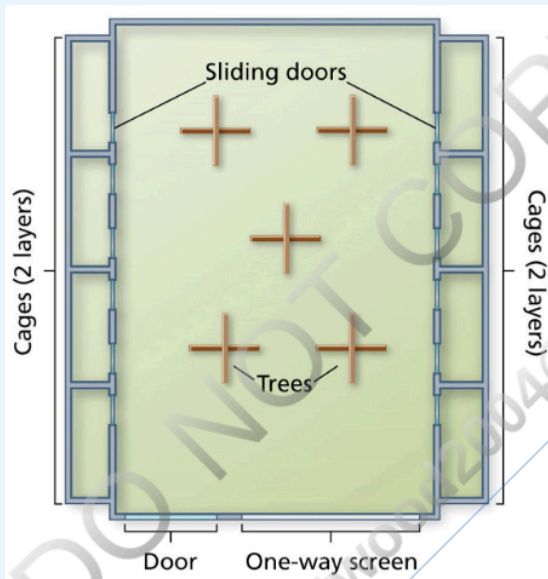


FIGURE 1. Test arena. Crosses indicate positions of artificial trees. (Source: Dingemanse et al. 2002)

### Results:

The parent-offspring regression on exploratory behavior was positive.



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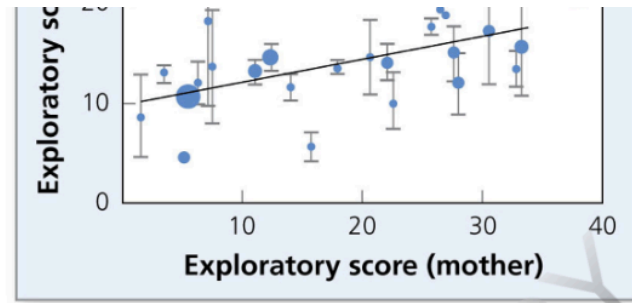


FIGURE 2. Parent-offspring regression. There was a positive correlation between parent and offspring (mean ± SE) behavior. Size of circles indicates number of individuals. (Source: Dingemanse et al. 2002)

### Conclusions:

Exploratory behavior has a genetic component and is a heritable trait.

### Evaluate

[Please note: You must be using an online, browser-based eReader in order to view this content.]

Can exploratory behavior evolve in a population of great tits? Draw a graph of the positive results of a selection experiment for bold and shy behavior.

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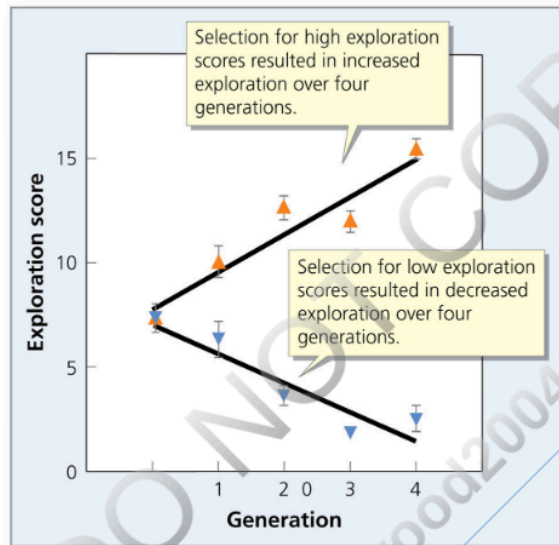
Find out more

Next, the research team conducted a selection experiment for fast and slow exploratory behavior by separating adults into two groups. One contained those birds with the lowest exploratory behavior scores, while the other contained those with the highest scores. Subsequent juveniles from these groups were chosen as the initial breeding generation for two selection lines. In each line, nine pairs of birds were used for breeding, and this

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breeding generation for two selection lines. In each line, nine pairs of birds were used for breeding, and this process was repeated for four generations. Researchers tested individuals from each generation to obtain their exploratory scores. The nine males and females with the highest (fast line) and lowest (slow line) scores of each generation were then selected for breeding. The research team found strong changes in the exploratory behavior of the two lines over four generations. By the fourth generation, the average exploratory score for individuals in the fast line was over four times higher than that for individuals in the slow line (Figure 4.21) (Drent, van Oers, & van Noordwijk 2003).



**FIGURE 4.21.** Selection experiment. The mean ( $\pm$  SE) exploratory score of individuals in the artificially selected lines for fast (orange) and slow (blue) exploration scores. (Source: Drent, van Oers, & van Noordwijk 2003)

Together, the results of these two experiments conclusively demonstrate that exploratory behavior in great tits is heritable. Not only does this mean that the existence of animal personalities can help to explain variation in behaviors among individuals in a population, but also that the behavioral variation within a single individual is constrained by its gene alleles. We illustrate how personalities constrain individual behavior with an example from salamanders.

#### Video: Personality in tits

[Please note: You must be using an online, browser-based eReader in order to view this content.]

Video: Personality in tits



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### FEATURED RESEARCH **Bold and shy personalities in streamside salamanders**

Streamside salamanders (*Ambystoma barbouri*) live primarily in the deep pools of shallow streams in eastern North America. The pools are separated by riffles, shallow areas of faster-flowing water, in which salamanders deposit eggs. Developing larvae face two challenges before they undergo metamorphosis and leave the stream. First, they must maximize feeding time to shorten their development time before the streams and pools dry up. Second, they must avoid predators such as the green sunfish (*Lepomis cyanellus*). When predators are present, larvae can seek shelter under rocks, but this behavior reduces time spent feeding.

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## CHAPTER SUMMARY AND BEYOND

Behavioral genetics is the study of the effects of genetic and environmental influences and their interactions on behavior. An important aspect of behavioral genetics is the identification of genes that contribute to large amounts of variation in behavior ([Fitzpatrick et al. 2005](#); [Pennisi 2005](#)). The knockout technique (in which a single gene is rendered nonfunctional) has greatly expanded our understanding of how single genes affect behavior. This technique is often used in animal models to gain insight into human pathologies ([van der Staay 2006](#)). Both QTL mapping and microarray analysis have been used to identify many genes that influence behavior ([Flint 2003](#)). York (2018) provides a recent review summarizing over 100 QTL studies on 30 species that identify genomic regions associated with behavioral variation. The next step underway is investigation of the expressed proteins associated with specific behaviors ([Valcu & Kempenaers 2015](#)).

While genes affect behavior, so too does the environment. The social environment is often manipulated to examine gene expression profiling ([Robinson, Fernald, & Clayton 2008](#)), most notably in birdsong. Recent work has begun to reveal how genotypic differences affect selective learning of the song of different tutors (e.g., [Mundinger 2010](#)). Multidisciplinary research has found behavioral, neural, and genetic parallels between human language development and birdsong development ([Prather, Okanoya, & Bolhuis 2017](#)). Identifying gene–environment interactions should help us better understand variation in behavior ([Bendesky & Bargmann 2011](#)).

Work on animal personalities has revealed how genotypes can limit behavioral variation among individuals ([Stamps & Groothuis 2010](#)). Recent work focuses on the ecological and evolutionary consequences of different personality traits ([Wolf & Weissing 2012](#); [Kern et al. 2016](#)) and the search for the genetic aspects of personality in humans ([Polderman et al. 2015](#); [Sanchez-Roige et al. 2018](#)).

## CHAPTER REVIEW

### 4.1 Behaviors vary in their heritability

- Animals display variation in their phenotype and genotype.
- Phenotypic variation can result from variation due to genes and the environment.
- The proportion of phenotypic variation in a trait due to genetic influences is its broad sense heritability.

### 4.2 Behavioral variation is associated with genetic variation

- Mutant yellow and wild-type genotype male fruit flies display different courtship behavior, demonstrating a link between genotype and behavior.
- A single major gene, *Gp-9*, influences social organization behavior in fire ants.
- An experimental knockout of the *V1aR* gene demonstrates its effect on mouse behavior under stress.
- QTL analysis identified genes associated with feeding behavior in aphids.

### 4.3 The environment influences behavior via gene expression

- Zebrafish siblings reared in different developmental environments display differences in aggressive behavior.
- Microarray analysis displayed differential gene expression in male fruit flies exposed to different social environments.
- An experimental knockdown of the *FoxP2* gene disrupted the normal development of zebra finch song.
- Rover and sitter fruit fly genotypes display different movement patterns in different feeding environments, demonstrating a gene–environment interaction.

### 4.4 Genomic approaches correlate gene expression with behavioral phenotypes

- Whole genome RNA analysis is used to examine differential gene expression across phenotypes.
- Honeybees and black-faced blennies provide examples of differential gene expression in different

phenotypes.

#### 4.5 Genes can limit behavioral flexibility

- Animal personalities are consistent differences in behavior over time or across different environmental conditions.
- Parent–offspring regression and selection experiments demonstrate that exploratory behavior is a heritable personality trait in great tits.
- Stream-side salamanders display consistent relative differences in activity level despite changes in predation risk, revealing activity level as a personality trait.
- A theoretical model shows that bold and shy personality traits can have equal fitness.
- Jumping spiders reared in different environments develop different levels of exploratory behavior.

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## CHAPTER 3

# Evolution and the Study of Animal Behavior

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 3.1 [Evolution by natural selection favors behavioral adaptations that enhance fitness](#)
- 3.2 [Modes of natural selection describe population changes](#)
- 3.3 [Individual and group selection have been used to explain cooperation](#)
- 3.4 [Sexual selection is a form of natural selection that focuses on the reproductive fitness of individuals](#)

### Features

- |                        |   |
|------------------------|---|
| Scientific Process     | 3.1 <a href="#">Stabilizing selection on territory size in cichlids</a> |
| Applying the Concepts  | 3.1 <a href="#">Do lemmings commit suicide?</a>                         |
| Toolbox                | 3.1 <a href="#">Genetics primer</a>                                     |
| Quantitative Reasoning | 3.1 <a href="#">Presence and absence of predator cues</a>               |

We enjoy watching birds at the feeders in our backyard. Finches, sparrows, chickadees, cardinals, and jays are regular visitors ([Figure 3.1](#)). Every so often, so too are Cooper's hawks (*Accipiter cooperii*), predators of small birds. One day, we were watching a group of finches at the feeder when a Cooper's hawk suddenly appeared and attacked. The finches scattered, fleeing quickly to dense shrubs. Three escaped, but one ended up in the hawk's talons. Such scenarios play out every day in nature—some individuals survive, while others do not. The same variation occurs during mating season: some individuals produce many offspring, while others produce few or none. Variation in survivorship and reproduction is the raw material for adaptive evolution.

NOTE: Variation in survivorship and reproduction is the raw material for adaptive evolution.



**FIGURE 3.1.** Birds at a feeder. Birds feeding are at risk of predation.

Evolutionary biologist Theodosius Dobzhansky once said, “Nothing in biology makes sense except in the light of evolution” (1973). This is because evolution is the foundation of our understanding of the natural world, and animal behavior is one important aspect of that world. In this chapter, we examine the process of evolution by natural selection. We start by describing natural selection in some detail and examining the conditions required for evolution to occur. Although natural selection results in changes in populations, it acts on individuals that collectively make up those populations, rather than on the populations themselves. Next we consider the evolution of cooperation and examine how selection can promote behaviors that benefit others. Finally, we introduce the concept of sexual selection, a form of natural selection that acts on reproduction and results in many of the morphological and behavioral differences that often exist between the sexes within a species.

### Video: Webcam of Bird Feeder

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Video: Webcam of bird feeder



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### 3.1 Evolution by natural selection favors behavioral adaptations that enhance fitness

#### Learning Objectives

After reading this section, you should be able to

- summarize the three conditions required for natural selection,
- design two types of experiments to measure the heritability of a trait,
- explain why individuals in populations vary in the traits they exhibit, and
- identify an example of an adaptation.

If you have ever visited a dog park, you've likely seen a variety of breeds, such as Boston terriers, Labrador retrievers, and greyhounds (Figure 3.2). All these breeds belong to the same species, *Canis lupus familiaris*, but each possesses unique traits with respect to body size and shape, tail length, head shape, coat texture, and color. The American Kennel Club currently recognizes almost two hundred dog breeds. Why are there so many, and where did they come from?





**FIGURE 3.2. Dog breeds.** There is tremendous variation in body size and morphology in these breeds. (a) Boston terrier; (b) Labrador retriever; (c) greyhound.

Dogs were the first domesticated species, but the exact date of the domestication process is still uncertain; it ranges from 14,200 YA (using archaeological evidence) to 36,000 YA (using genetic data) (Botigue et al 2017). All dog breeds diverged from gray wolf (*Canis lupus*) ancestors as a result of human manipulation of the breeding of individuals (Akey et al. 2010). Over many generations, human breeders have selected individuals that possess certain traits for a particular breed, called the breed standard. Many breeds were created for specific tasks: terriers to hunt vermin, retrievers to find and retrieve hunters' birds, and greyhounds to hunt swift prey. Breeders allowed reproduction only among individuals that possessed certain traits. Differences in breed standards over time eventually led to ever-greater differences among the breeds we see today. This process is known as artificial selection because it is done "artificially"—that is, by humans.

Charles Darwin's great insight was that a similar process also occurs naturally, a process that he called natural selection. **Natural selection** is a process in which some individuals in a population survive and reproduce, while others do not. It is the mechanism that results in adaptive evolution. Darwin was not the first to suggest that species evolve, but he (along with Alfred Russell Wallace) was the first to describe the plausible mechanism, natural selection, by which evolution can occur.

Natural selection occurs because there is variation in traits among individuals in a population, and some traits provide individuals with greater reproductive success. When these traits are **heritable**, they are passed genetically from parents to offspring. Natural selection can result in changes in allele frequencies in a population over time—a process that we recognize as **evolution**.

In his book *On the Origin of Species* (1859), Darwin articulated three conditions required for evolution by natural selection:

1. Variation exists among individuals in a population in the traits they possess.
2. Individuals' different traits are at least partly heritable. Traits can be passed from parents to their offspring so that offspring resemble their parents in the traits they possess.
3. Traits confer differences in survivorship and reproduction, a measure we call **fitness**: individuals with certain traits will have higher fitness, while those with other traits will have lower fitness relative to one another. Therefore, the fitness of individuals is not random; it is based on the traits they possess.

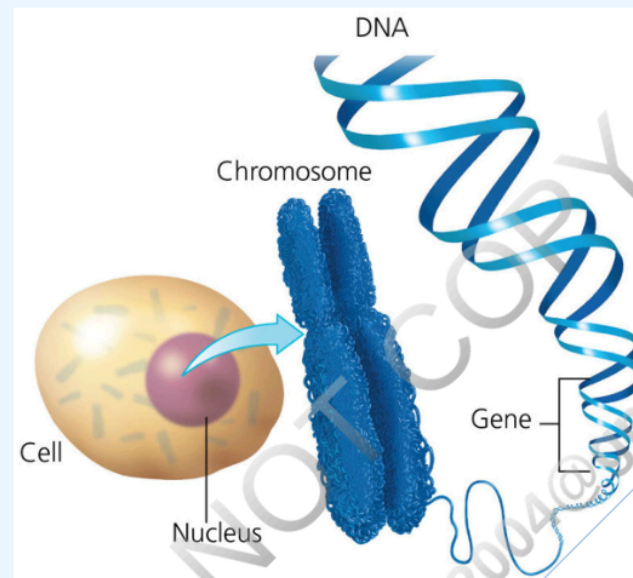
Today, we know that gene alleles are the basis of most phenotypic traits (Toolbox 3.1). Random mutations introduce new alleles into populations. Natural selection acts on heritable variation among individuals and can result in changes in allele frequencies and associated trait values in a population. Traits that confer high fitness increase over time, while those that confer low fitness decline, resulting in evolutionary changes.

### TOOLBOX 3.1 Genetics primer

Deoxyribonucleic acid (DNA) condenses to form chromosomes during mitosis and meiosis.

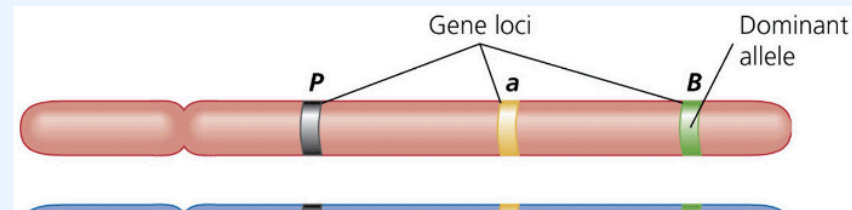
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Deoxyribonucleic acid (DNA) condenses to form chromosomes during mitosis and meiosis (Figure 1). Specific stretches of DNA contain genes, which code for polypeptides (e.g., proteins) that have a variety of functions.



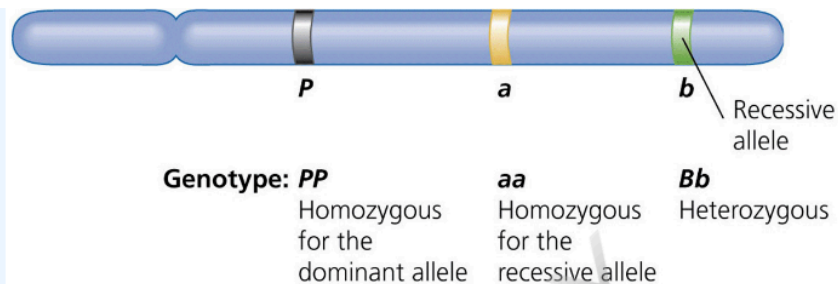
**FIGURE 1. DNA.** DNA consists of two helical chains that condense to form chromosomes during mitosis and meiosis. Genes are found in specific stretches of DNA and code for polypeptides.

Alleles are different versions of a gene (Figure 2), while the locus is the physical location of an allele on a chromosome. Diploid organisms have two copies of each chromosome, and each may have a different allele. If the alleles are the same, the organisms are homozygous for these alleles; if the alleles are different, they are heterozygous. During sexual reproduction, each parent contributes only one of its alleles. Therefore, offspring have different allele combinations than their parents. When natural selection acts such that some individuals reproduce more than others, more alleles of the individuals who reproduce may be present in the next generation. Thus, selection can result in changes in the frequency of alleles in a population.



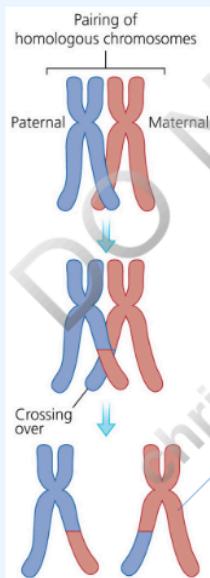
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**FIGURE 2. Alleles on chromosomes.** The locus (pl., loci) is the physical location of a gene on a chromosome. Alleles at a gene locus can be different versions of the gene.

During meiosis, homologous chromosomes line up in pairs (Figure 3) and can exchange segments of DNA, a process known as crossing over. This action results in novel combinations of DNA that increase genetic diversity and can increase the variation of traits among individuals in a population, a required condition for evolution by natural selection.



**FIGURE 3. Recombination.** Homologous chromosomes can exchange segments of DNA.

When traits are heritable, parents will tend to pass on the traits they possess to their offspring via their shared alleles. Many behavioral traits that have been studied are in fact heritable, including mating behavior, feeding behavior, overall activity level, and aggression (Stirling, Réale, & Roff 2002; Croston et al. 2015). In the next section, we examine how researchers study the heritability of behavioral traits.

## Measures of heritability

How do we quantify the heritability of a trait? Two methods are commonly used:

1. **Parent-offspring regression** analysis examines the similarity between parents and their offspring in terms of their traits. If a trait is heritable, the trait values of offspring should be similar to the trait values of their parents; that is, there should be a positive relationship between offspring and parent trait values. In this method, offspring trait values are plotted against parent trait values, and the slope of the resulting regression indicates the heritability of the trait.
2. In the **selection experiment** method, different groups of individuals are subjected to differential selection on the trait in question. If artificial selection acting on a trait results in changes in the average trait value in subsequent generations, the trait is heritable.

Let's examine one case study in which both methods were used to determine the heritability of a behavioral trait—maternal defense behavior.

## FEATURED RESEARCH Maternal defense behavior in mice

Stephen Gammie, Theodore Garland, and Sharon Stevenson examined the heritability of maternal defense behavior in mice (Gammie, Garland, & Stevenson 2006). In many rodents, nesting females with pups will aggressively attack conspecific intruders, particularly unfamiliar males that represent a threat to offspring (Agrell, Wolff, & Ylonen 1998). Because female domestic mice (*Mus domesticus*) differ in their level of maternal aggressiveness, the researchers investigated whether such behavior might be heritable.

### Video: Maternal aggression toward intruders

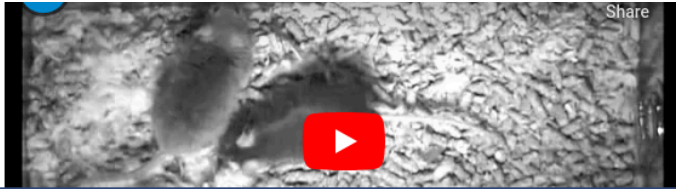
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Video: Maternal aggression toward intruders

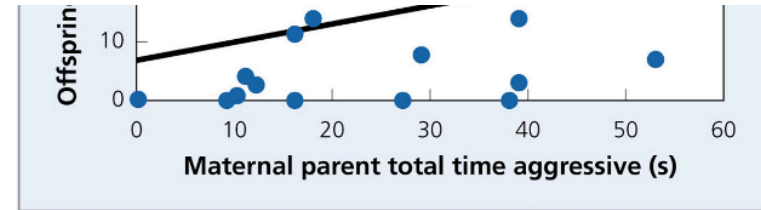
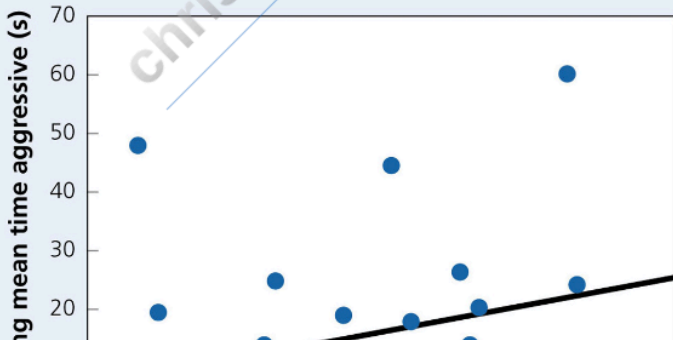


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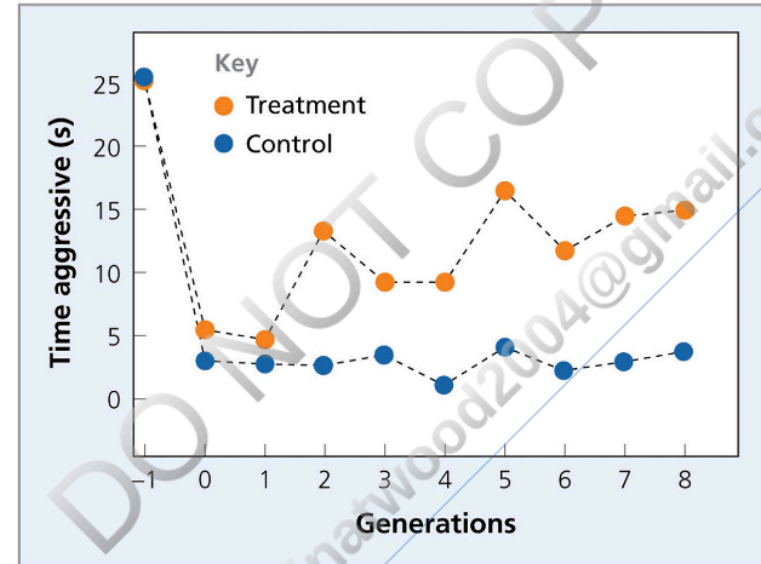
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Find out more

The team conducted both a parent-offspring regression analysis and a selection experiment. They started with 26 females and 26 males. For the selection experiment, half were randomly assigned as the control line and the other half the selection line. After each pair mated and the female was impregnated, each female was housed alone through parturition. At 4–6 days post-partum, each female was scored for maternal defense behavior by placing an unfamiliar male in her home cage. Over a three-minute test, the researchers recorded the total duration of her attacks on the male. In the selection line, only the offspring of the female with the longest total duration of attacks on the male (i.e., the highest level of maternal defense behavior) were allowed to mate and have offspring. In the control line, offspring of a randomly selected female were allowed to mate and have offspring. This protocol continued for eight generations. For the parent-offspring regression analysis the researchers analyzed the maternal aggression behavior of the initial parental generation and their offspring. They found a significant positive correlation between a mother's defense score and that of her daughters (Figure 3.3). The selection experiment indicated a significant increase in maternal defense behavior in the treatment family lines over the eight generations relative to control females (Figure 3.4). The results of both experiments conclusively demonstrate that maternal defense behavior in mice is a heritable trait.



**FIGURE 3.3. Mouse parent-offspring regression.** There was a positive correlation between maternal and offspring defensive aggression behavior. (Source: [Gammie et al. 2006](#))



**FIGURE 3.4. Mouse selection experiment.** Mean levels of aggression in control (blue) and treatment (orange) selection lines over generations. (Source: [Gammie et al. 2006](#))

## Variation within a population

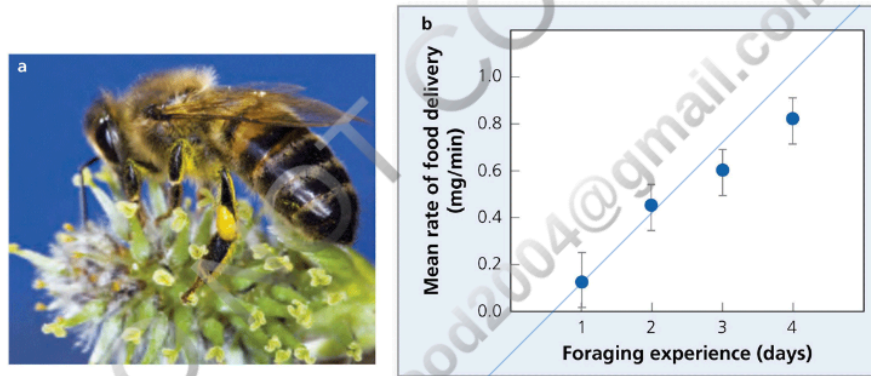
Through the process of natural selection, populations evolve. But we still observe much variation in the traits that individuals possess. Why do individuals in populations vary in behavior?

First, as we just saw, individuals differ in their genetic composition. Each generation introduces new variation into populations through gene recombination, the immigration of new alleles into a population, and mutations ([Hartl 2000](#)). Because individuals in any population differ genetically, they also tend to vary in their behavior. Furthermore, changes in environmental conditions can change the fitness of different traits and so maintain much variation in the frequencies of different alleles.

variation in the frequencies of different alleles.

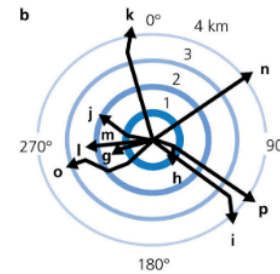
Second, many behaviors develop as a consequence of both genetic and environmental effects. Thus, even close relatives (with similar genes) often exhibit very different behavior as adults when they are exposed to different environmental conditions as juveniles. We will examine this issue in more detail in [Chapter 4](#).

Third, many complex behaviors require learning and so are modified with experience. Because individuals will differ in experience over the course of a lifetime, we will observe differences in their behavior as well. For example, bees need to learn how best to extract nectar and pollen from flowers and then transport them efficiently back to the colony. [Dukas \(2008\)](#) showed that the feeding performance of honeybees (*Apis mellifera*)—that is, their rate of food delivery to the colony—increases dramatically over the first four days of foraging activity as a result of trial-and-error learning. An individual bee delivers food to the colony on its fourth day of activity at a rate almost four times higher than its rate on its first day ([Figure 3.5](#)).



**FIGURE 3.5. Honeybee food delivery.** (a) Honey bee. (b) The mean ( $\pm$  SE) rate of food delivery for bees with different experience. Each day, the rate increased, indicating that honeybees gain experience through trial-and-error learning. (Source: [Dukas 2008](#))

Fourth, there might be little or no variation in fitness over a wide range of behaviors. One example is dispersal behavior. Dispersal is the process of moving away from the natal area, or place of birth, to find an adult breeding area or territory. For many species in many habitats, individuals will experience the same fitness whether they disperse north, south, east, or west. When this is true, we expect to see much variation in dispersal direction within a population. For example, James Belthoff and Gary Ritchison examined the dispersal direction of Eastern screech owls (*Otus asio*) ([Figure 3.6](#)) ([Belthoff & Ritchison 1989](#)). They fitted nestlings with radio transmitters and located individuals several times per week as the birds dispersed from their natal territory. The researchers found that there was no particular pattern with respect to dispersal direction, which we would expect if characteristics that determine territory quality and fitness are not associated with compass direction relative to the natal location ([Figure 3.6](#)).



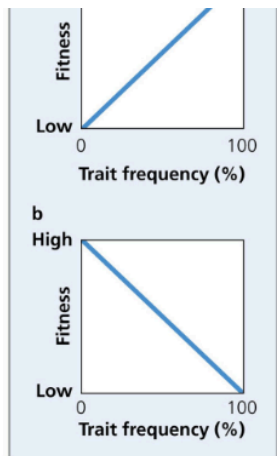
**FIGURE 3.6. Owl dispersal.** (a) Screech-owl. (b) Each line represents the dispersal direction and movement distance of one individual. Individuals (letters) dispersed in all directions. (Source: [Belthoff & Ritchison 1989](#))

Fifth, individuals in all populations typically differ in size, nutritional status, health, and other traits. These differences can lead to significant variation in behaviors. For instance, many male birds sing complex songs. While song production has a strong genetic component, it also requires learning and can be physically demanding. Thus, in several species, vocal performance increases with age: older males that are in better condition produce different songs from younger males (e.g., [Ballantine 2009](#)).

Finally, the fitness of a trait (behavior) may be related to its frequency. In **frequency-dependent selection**, the fitness of a trait depends on its frequency in a population relative to other **phenotypes** (characteristics of an organism). In positive frequency-dependent selection, the fitness of a phenotype increases as it becomes more common ([Figure 3.7a](#)); in negative frequency-dependent selection, fitness declines as a phenotype increases in frequency ([Figure 3.7b](#)). Negative frequency-dependent selection can maintain different behaviors in a population. For example, some male fish defend territories to attract and mate with females, while others hide at the edge of these territories and attempt to fertilize the eggs of females attracted to the territory holder. Such “sneaker” male behavior is frequency dependent: it results in high fitness when most males in a population defend territories (a scenario that produces many opportunities to fertilize eggs), but much lower fitness when few males defend territories (producing fewer opportunities for reproduction). As another example, let’s examine a research study that investigated frequency-dependent selection in relation to bird predation.





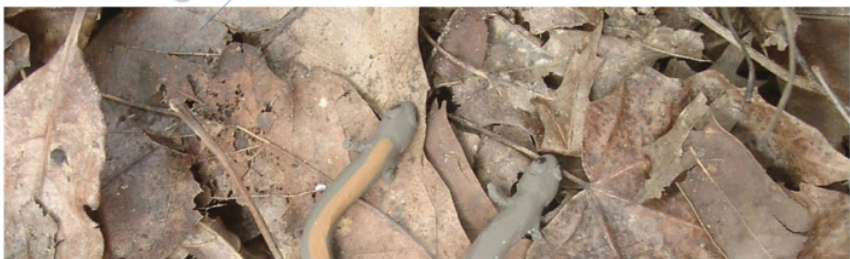


**FIGURE 3.7. Frequency-dependent selection.** (a) In positive frequency-dependent selection, the fitness of a trait increases as it becomes more common in a population. (b) In negative frequency-dependent selection, the fitness of a trait declines as it becomes more common in a population.

## FEATURED RESEARCH Frequency-dependent selection

Benjamin Fitzpatrick and two high school students, Kim Shook and Reuben Izally, examined frequency-dependent selection in birds foraging on salamanders (Fitzpatrick, Shook, & Izally 2009). The researchers noted that numerous species of small, slender, cryptic salamanders that live on the forest floor throughout North America all have a similar polymorphism. Within each species, some individuals have a dorsal stripe, while others do not.

The research team investigated whether frequency-dependent selection as a result of bird predation maintains this polymorphism. They used a mold to create model salamanders out of clay, some of which possessed an ochre-colored dorsal stripe (Figure 3.8). Using edible library paste, the team attached a food reward (half a peanut) to the underside of each model; they then put the models on trays filled with leaf litter and placed the trays in an open area next to a woodlot.



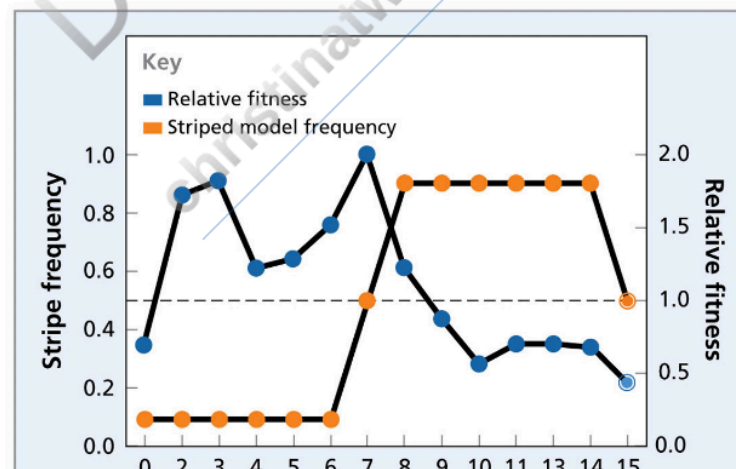
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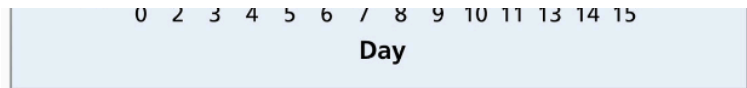
**FIGURE 3.8. Salamander models.** A striped and an unstriped model used in Fitzpatrick, Shook, and Izally's experiment.

To examine how relative frequency affected the fitness of each model, the research team varied their abundances: for the first six days, the ratio of striped to unstriped salamander models was 5:45, followed by one day of equal numbers of both morphs. For the next six days, the ratio was reversed (45:5), followed by one final day of equal abundances. The researchers quantified survival by counting the number of model salamanders that still had their food reward at the end of each day.

The team observed several blue jays (*Cyanocitta cristata*) foraging on the models, so they could confirm that the models were preyed upon. Fitzpatrick and colleagues found that when a morph occurred at low relative frequency, it had higher relative survivorship (Figure 3.9); when it occurred at high relative frequency, it had low relative survivorship. The rare form always had a survival advantage, whether striped or unstriped. Therefore, frequency did affect survivorship and was negatively frequency dependent, but the presence of the stripe did not affect survival. This may explain how this morphological polymorphism is maintained within a species.



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**FIGURE 3.9. Frequency and fitness.** The daily frequency of striped models (orange) and their relative fitness (blue). (Source: Fitzpatrick, Shook, & Izalzy 2009)

These examples show that a variety of complex factors contribute to variation in behavior within a population. Indeed, evolution by natural selection requires such variation.

## Fitness and adaptation

As we have just seen, there is trait variation among individuals in a population. Those traits might be a particular morphology, physiology, or behavior. In general, some traits confer higher fitness (survivorship and reproduction) than others. Traits that result from natural selection and have been selected for their current function are called **adaptations**. Individuals with these traits will tend to survive better and leave more offspring than individuals whose traits do not confer a selective advantage (i.e., yield lower fitness); thus, adaptations are identified relative to existing traits in a population (Reeve & Sherman 1993).

The most direct measure of an individual's fitness is the number of its progeny that go on to reproduce. However, few studies, particularly those that focus on behavior, measure fitness in this way. For one thing, this approach can be both logistically difficult and time consuming. Instead, most studies use indirect measures of fitness. Behavioral researchers often estimate fitness by quantifying parameters such as survivorship, number of mates, body size, growth rate, and feeding efficiency. Such indirect measures are typically positively correlated with more direct fitness measurements (e.g., Ritchie 1990; Taylor et al. 2008).

In this section, we've seen how evolution by natural selection favors behavioral adaptations that enhance fitness. Next, we examine in more detail how traits in populations change over time.

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In this section, we've seen how evolution by natural selection favors behavioral adaptations that enhance fitness. Next, we examine in more detail how traits in populations change over time.

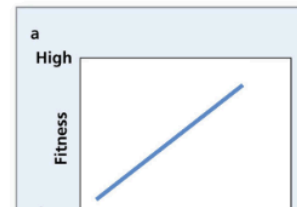
## 3.2 Modes of natural selection describe population changes

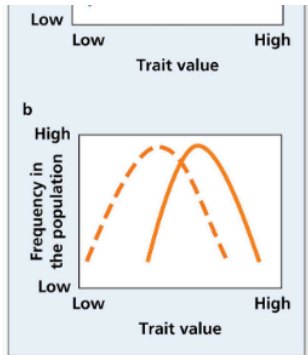
### Learning Objectives

After reading this section, you should be able to

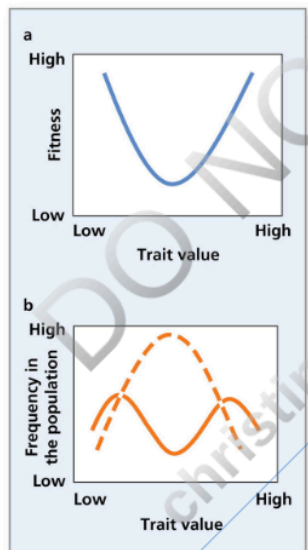
- diagram and summarize directional, stabilizing, and disruptive selection; and
- explain how researchers use the cost-benefit approach to study adaptations.

Natural selection can cause a change in the frequency of traits in a population over time and so provides an explanation for evolutionary changes. Evolutionary biologists have identified three modes of natural selection that describe how populations change as a result of the relative fitness values of different trait values. To illustrate this process, consider a population of snails in which individuals exhibit continuous variation in color, ranging from white to pink to red. **Directional selection** occurs when individuals with one extreme trait value possess the highest fitness (Figure 3.10). In this case, let's say red individuals have the highest fitness in a particular environment; as a result, their frequency in the population will increase. **Disruptive selection** occurs when individuals with either of two extreme trait values have the highest fitness (Figure 3.11). The red and white individuals both have higher fitness than pink individuals in the same environment. Hence, the frequency of red and white individuals will increase, while the frequency of pink individuals will decline. Last, **stabilizing selection** occurs when individuals with intermediate trait values—in this instance, pink—have the highest fitness in a particular environment (Figure 3.12). When stabilizing selection is at work, the frequency of pink individuals will increase over time. Let's examine one example of each mode of selection.

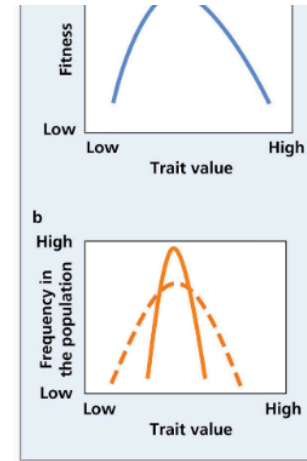




**FIGURE 3.10. Directional selection.** (a) Individuals with high trait values have higher fitness than individuals with low trait values. (b) The dashed line is the population before selection. The solid line is the population after selection.



**FIGURE 3.11. Disruptive selection.** (a) Individuals with low and high trait values have the highest fitness. (b) The dashed line is the population before selection. The solid line is the population after selection.



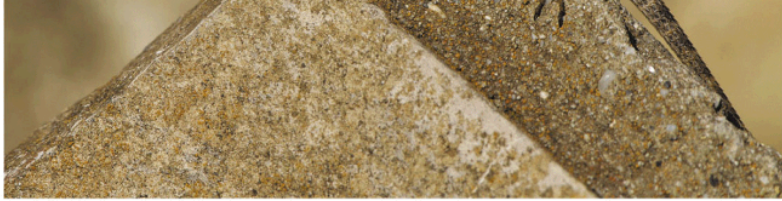
**FIGURE 3.12. Stabilizing selection.** (a) Individuals with intermediate trait values have the highest fitness. (b) The dashed line is the population before selection. The solid line is the population after selection.

## FEATURED RESEARCH Directional selection in juvenile ornate tree lizards

For many animals, the ability to move quickly affects survival: faster individuals can evade predators better and capture mobile prey more effectively than their slower counterparts. Therefore, we might expect directional selection to act on the speed of movement. Donald Miles examined this idea by studying selection on locomotor performance in juvenile ornate tree lizards (*Urosaurus ornatus*) (Miles 2004). Found in a variety of habitats in southwestern North America, these small lizards (less than 6 cm in snout-vent length) feed on a diverse array of insects and are preyed upon by larger lizards, snakes, and birds (Figure 3.13).







**FIGURE 3.13. Ornate tree lizard.** These lizards are common in southwestern North America.

Miles collected 45 juveniles from one population near Tucson, Arizona, and quantified their locomotor performance in the laboratory. All individuals were tested for two days using a 2 m long raceway with a sand floor. Individuals were gently prodded to run the length of the track. Eight infrared photocells, spaced at 25 cm intervals, recorded their movement and allowed the calculation of mean velocity (average speed over 2 m) and burst velocity (fastest speed over a 25 cm interval). Miles repeated this test eight times for each lizard, giving it one hour to recover between trials. He also recorded the body size and mass of each individual, as well as its stride length, which was measured by the distance between successive footfalls in the sand. All individuals were uniquely marked and later released back into the wild at their capture site. Miles then recorded the survival of these individuals over the next six months by visiting the site repeatedly and recapturing surviving individuals. He used survivorship over this time period as a measure of fitness.

Miles found that larger, heavier individuals had high survivorship, as did those with higher mean velocity, higher burst velocity, and longer stride length (Table 3.1). Body size and speed are often correlated, with larger individuals tending to move faster, so which trait was more important in this case? Miles used a regression analysis to determine that locomotor performance was more important than body length in affecting survival. Locomotor performance is a function of stride length (Bonine & Garland 1999). He concluded that in this population, there was strong directional selection on limb length in juveniles: longer limbs produce longer strides that allow individuals to achieve greater velocities, thereby enhancing their survivorship.

**TABLE 3.1 Lizard traits.** Mean ( $\pm$  SE) trait differences between survivors and nonsurvivors. Survivors had higher values for all traits.

Trait	Survivors	Nonsurvivors
Snout-vent length (mm)	36.6 $\pm$ 3.5	33.6 $\pm$ 4.2
Mass (g)	1.36 $\pm$ 0.43	1.13 $\pm$ 0.46
Initial velocity (m/s)	0.36 $\pm$ 0.16	0.35 $\pm$ 0.15
Burst velocity (m/s)	0.62 $\pm$ 0.18	0.48 $\pm$ 0.14
Mean velocity (m/s)	0.39 $\pm$ 0.14	0.29 $\pm$ 0.11
Stride length (mm)	89.4 $\pm$ 14.6	71.8 $\pm$ 13.1

(Source: Miles 2004).

## FEATURED RESEARCH Disruptive selection in spadefoot toad tadpoles

Disruptive selection can occur when individuals in a population specialize on different resource types and there is **competition** for those resources, a situation known as intraspecific competition. Imagine a population of individuals that feed on seeds ranging in size from small to large. Assume that the individuals differ in the type of seeds they consume: one-third eats only small seeds; one-third, intermediate; and one-third, large. If intermediate seeds are rare in the environment, individuals that specialize on them will have the lowest fitness as a result of increased competition for food. Individuals that eat the extremes (either small or large seeds) will have higher fitness and should increase in the population. David Pfennig and colleagues, who have studied disruptive selection in New Mexican spadefoot toad tadpoles (*Spea multiplicata*), examined a similar scenario in several experiments (Pfennig & Pfennig 2005; Pfennig, Rice, & Martin 2007; Martin & Pfennig 2009).

Spadefoot toads are small amphibians (less than 6 cm in length) that live in a variety of habitats in North America. In arid regions of southwestern North America, they breed in temporary rain-filled ponds created by intense summer rainstorms. Once a pond fills with water, eggs hatch and the emerging tadpoles feed in the pond while they grow and develop over a span of three weeks. They consume both detritus (decomposing organic material) and small invertebrates that are typically found in such environments. Within a single pond population, individuals exhibit a wide range of variation in feeding morphology and behavior. Some individuals (omnivore morphs) feed mainly on detritus on the pond bottom; they have round bodies, smooth mouthparts, and small jaw muscles (Figure 3.14). Other individuals (carnivore morphs) specialize on invertebrates; they have narrower elongated bodies, notched mouthparts, and large jaw muscles. A third group (intermediate morphs) consume both detritus and invertebrates; they possess morphology that is intermediate between that of the two specialists.



**FIGURE 3.14. Spadefoot toad tadpoles.** Omnivore morph (top) and carnivore morph (bottom).

Pfennig and colleagues hypothesized that disruptive selection may be operating on tadpole morphology and feeding behavior. Previous work had demonstrated that tadpoles compete for food (Pfennig 1992). Specialized morphs should experience lower competition, because they compete for food with only a subset of the population—their own morphs and intermediate morphs, but not other specialist morph individuals. In contrast, intermediate morph individuals compete with all individuals in the population.

To evaluate their hypothesis, Pfennig's research team tested two predictions:

**Prediction 1:** Omnivore morphs would feed more efficiently than intermediate morphs on detritus; carnivore morphs would feed more efficiently than intermediate morphs on invertebrates.

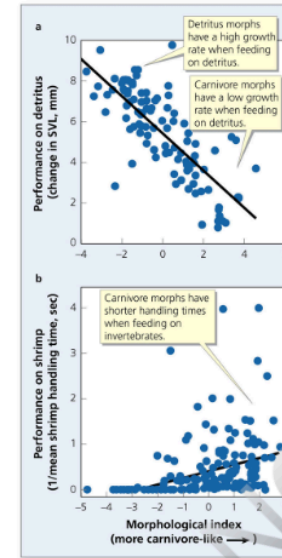
**Prediction 2:** Omnivore and carnivore morphs would have higher fitness than intermediate morphs.

To test the first prediction, the researchers examined the feeding efficiency of tadpoles forced to consume only one food type. In one experiment, they placed lone individuals in small wading pools within cages and allowed them to feed on detritus for eight days. The researchers measured the size of each individual (snout-vent length) at the beginning and end of the experiment to determine its growth rate, which was used as a measure of fitness. The morphology of each individual was quantified (smooth or notched mouth and the width of jaw muscles) to provide a continuous morphology index that ranged from "omnivore morph" through "intermediate" to "carnivore morph." In a second experiment, the research team characterized the feeding performance of individuals on invertebrates by placing lone tadpoles in small containers with ten fairy shrimp (*Thamnocephalus* sp.), a common invertebrate food item for tadpoles. The researchers measured the amount of time that individuals required to capture and eat the shrimp, an important aspect of feeding efficiency. They measured the morphology of each individual in this experiment to create a morphology index.

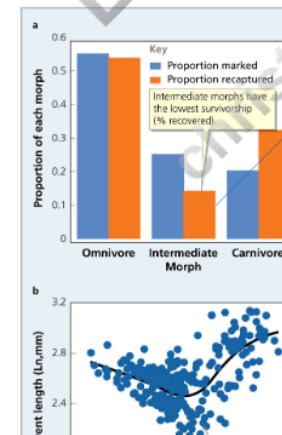
To test the second prediction, the research team marked over 500 individuals from one pond 11 days after it had been filled with water and spadefoot toad eggs had hatched. They measured each individual to quantify a morphology index and then categorized individuals into one of three types: omnivore morph, carnivore morph, or intermediate morph. Individuals of each morph type were marked with a different color elastomer tag, which was injected under the skin, and were then returned to the pond to continue their development. Eight days later, the researchers collected 1,500 individuals from the pond (including many marked individuals) and counted the number of each color to obtain an estimate of each morph's survivorship (one measure of fitness). To obtain a second measure of fitness, the research team also examined 301 unmarked tadpoles from the 1,500 collected. For each, they quantified its morphology index and recorded its size (snout-vent length). Body size in developing tadpoles is correlated with fitness: larger individuals have higher survivorship and fitness (Pfennig & Pfennig 2005).

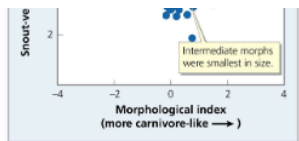
The researchers found that the feeding performance of each specialized morph was higher than that of intermediate morphs, as they had predicted. For individuals feeding on detritus, omnivore morph individuals exhibited higher growth rates than intermediate morphs, and carnivore morphs fed more efficiently on invertebrate prey than did intermediate morphs (Figure 3.15). In addition, both measures of fitness indicated that intermediate

morphs had lower fitness than either specialized morph. Intermediate morphs also had a lower probability of survival (indicated by a significantly lower recapture rate) than both omnivore and carnivore morphs. Among the unmarked individuals, intermediate morphs were smaller than both specialized morphs (Figure 3.16).



**FIGURE 3.15. Tadpole feeding performance.** (a) Growth rate of individuals feeding on detritus as a function of their morphology. Individuals with more carnivore-like morphology showed slower growth. (b) Performance of individuals feeding on shrimp as a function of their morphology. Individuals with more carnivore-like morphology had shorter handling times. (Source: Martin & Pfennig 2009)





**FIGURE 3.16. Tadpole survivorship and size.** (a) The proportion of each morph type recovered in the mark-recapture study. Intermediate morphs had the lowest survival. (b) Unmarked individuals of intermediate morphology were the smallest size, a measure of fitness. (Source: [Martin & Pfennig 2009](#))

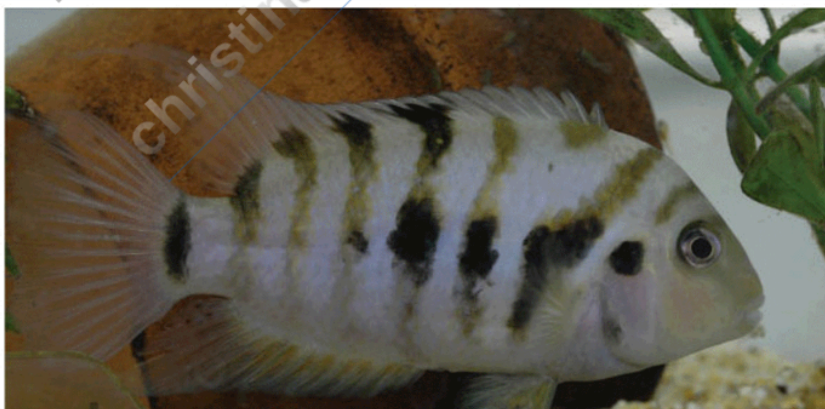
The research team concluded that their results supported their hypothesis. Intermediate morph individuals had lower fitness (lower survival and smaller body size) than either omnivore morph or carnivore morph individuals, likely because of competition, an example of disruptive selection. Individuals with specialized morphology had fewer competitors and were more efficient feeders than individuals with intermediate morphology.

## FEATURED RESEARCH Stabilizing selection in juvenile convict cichlids

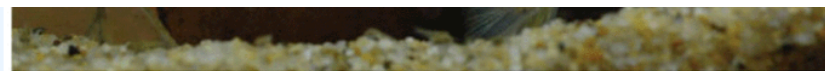
To understand stabilizing selection, let's consider territorial defense behavior. Many animals defend a territory to protect the food it contains or to attract mates. This defense requires time and energy to fight off potential intruders, and these costs increase as territory size increases. Thus, one might anticipate that there would be a territory size of intermediate value that would lead to the highest fitness. Jason Prawn and James Grant examined this hypothesis in juvenile convict cichlids (*Amatitlania nigrofasciata*) ([Prawn & Grant 1999](#)) ([Scientific Process 3.1](#)).

### SCIENTIFIC PROCESS 3.1

#### Stabilizing selection on territory size in cichlids



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Research Question: *How does territory size in cichlids affect fitness?*

### Hypothesis:

An intermediate territory size will optimize fitness.

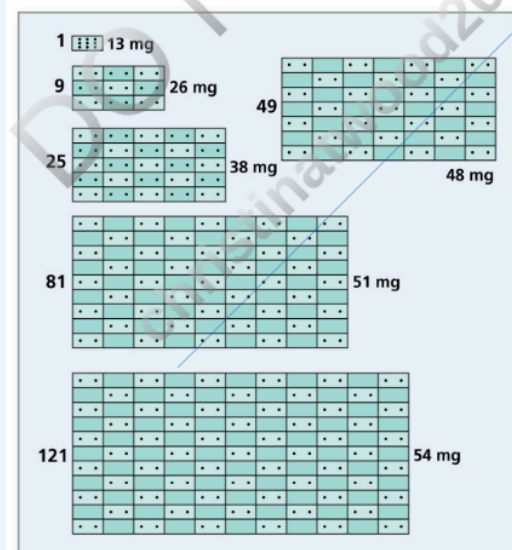
### Prediction:

Individuals that defend an intermediate-sized territory will have the highest growth rate.

### Methods:

The researchers:

- Created different-sized food patches
- Placed one patch in an aquarium with a single dominant (focal) fish
- Added four intruders to each aquarium and recorded the territorial defense behavior of the dominant fish and its growth rate



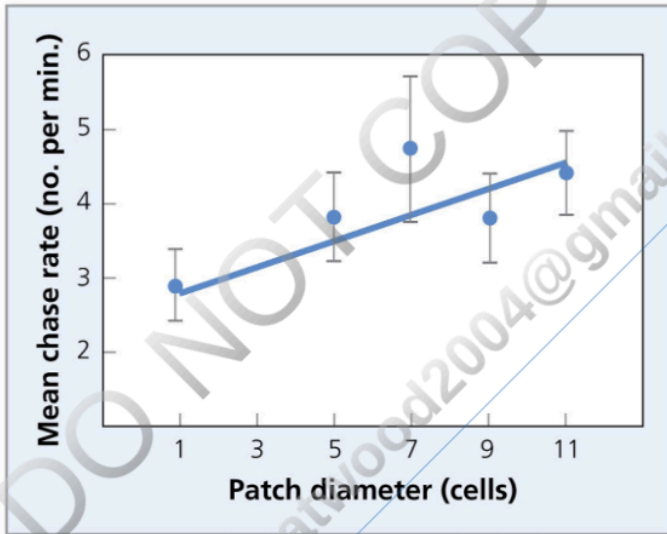
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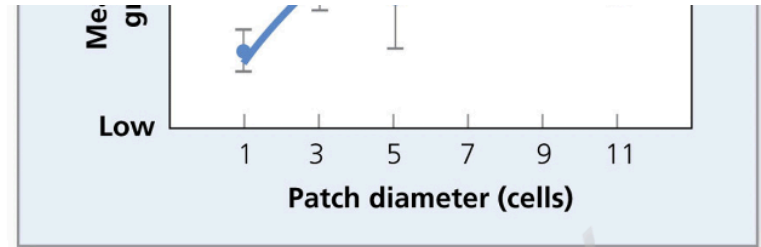
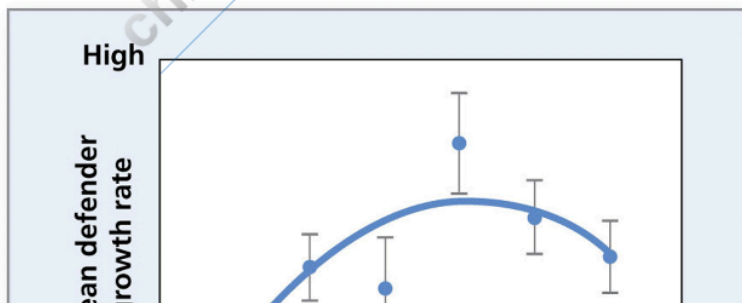
**FIGURE 1. Experimental territories.** Each rectangle represents a cell; food is indicated by dots. Patches contain 13–54 mg of food. (Source: [Praw & Grant 1999](#))

### Results:

- The focal fish defended the entire food patch from intruders.
- Defense behavior increased as territory size increased.
- Fish defending intermediate-sized territories had the highest growth rate.



**FIGURE 2. Patch defense.** The chase rate increased with territory size. (Source: [Praw & Grant 1999](#))



**FIGURE 3. Growth rate.** Fish in intermediate-sized territories had the highest growth rate. (Source: [Praw & Grant 1999](#))

### Conclusion:

Selection will favor individuals that defend intermediate-sized territories, because they will have the highest fitness.

### Evaluate

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Convict cichlids are a common aquarium fish native to Central America. Individuals frequently defend small territories and feed on a variety of foods, including invertebrates, small fish, plants, and algae. To examine territory defense, Praw and Grant used aquaria that contained a single food patch consisting of different numbers of ice cube tray cells. Six patch sizes were used, ranging from one to 121 cells. Commercial fish food pellets were evenly distributed across each patch, which meant that larger patches contained more food than smaller ones.

The researchers allowed a single large, dominant fish to defend a territory around the food patch. These individuals always attempted to defend the entire food patch, which varied in size. Next, the researchers introduced four small, subordinate intruder fish into each aquarium. Intruders attempted to feed from the food patch while the dominant fish defended its territory. For each dominant fish, Praw and Grant recorded the amount of food it ate, the number of intruder chases, and its growth rate over a ten-day period. Because all fish were juveniles (and did not exhibit mating behavior), the researchers focused on growth rate as a measure of fitness. In general, juvenile fish with high growth rates have higher fitness.

The researchers found that fish that defended very small or very large territories had lower growth rates than fish that defended intermediate-sized territories. This occurred because fish that defended very small territories had less food to eat, while those that defended very large territories spent much more time and energy chasing intruders. Individuals that defended intermediate-sized territories had more to eat than fish that defended small territories (and so grew faster) but spent less time (and thus energy) chasing intruders than fish with large territories. From this experiment, Praw and Grant concluded that selection would favor individuals that defend territories of intermediate size.

Studying adaptation: the cost-benefit approach

Under all modes of selection, the trait value that confers the highest fitness in a particular environment is called the **optimal trait value**. If the trait under selection is heritable, and if the selection regime remains constant, populations will evolve toward the optimal trait value (or values) over successive generations. Thus, we see that natural selection is an optimizing process that allows us to understand adaptations by describing the fitness benefits and costs of different phenotypes. This **cost-benefit approach** illustrates a common ultimate explanation method used to study behavioral adaptations: identify fitness costs and benefits of different traits to determine which trait has the highest net benefit.

The simplest cost-benefit approach predicts that a behavior that maximizes fitness, irrespective of how other animals behave, will continue to be passed down from parent to offspring. However, in many situations, the fitness of a behavior will depend on how others behave. Determining the behavior that maximizes fitness in such cases requires the use of **game theory**—a more sophisticated cost-benefit approach, first developed in economics, that finds the best solution to an interaction or game between two players (Parker & Hammerstein 1985). These models take into account the players, the strategies they adopt, and the payoffs for each one. In economics, the players are people, the strategies are different behaviors, and the payoffs are typically monetary. John Maynard Smith and George Price were the first scientists to apply game theory to animal behavior (Maynard Smith & Price 1973). In these cases, the players are animals and the strategies are again different behaviors, but the payoffs are described in terms of fitness.

The solution to biological games is the **evolutionary stable strategy (ESS)**; this strategy (a single behavior or multiple behaviors observed in different proportions in the population) cannot be beaten by any alternative strategy, and no player will adopt a different strategy because doing so will result in a lower payoff. Oftentimes, when the fitness of a behavior depends on the behavior of others, fitness will be frequency dependent. Game theory is used to predict the proportion of each behavior that one should observe in a population (Maynard Smith 1982; Riechert & Hammerstein 1983).

We will see the cost-benefit approach, as well as several examples of game theory, used throughout this book. In fact, we have already seen the cost-benefit approach in Chapter 2, when Lima and his colleagues used it as an ultimate explanation for the food-carrying behavior of squirrels that maximizes their fitness.

### 3.3 Individual and group selection have been used to explain cooperation

#### Learning Objectives:

After reading this section, you should be able to

- distinguish between individual and group selection,
- differentiate between direct and inclusive fitness, and

- explain how kin selection can explain the evolution of cooperation.

In the lizard, spadefoot toad, and fish examples described previously, natural selection was assumed to act on individuals. As noted, those individuals that have the highest fitness are more likely to pass their genes and behavior on to the next generation. However, some behavior is not so readily explained by **individual selection**—natural selection at the level of individuals. Many social animals display cooperative behavior, helping others to survive and reproduce. For example, several social insect colonies (e.g., those of bees, termites, and wasps) contain many sterile workers and a single queen who reproduces. The workers defend the colony and deliver food to the queen and her offspring. Why should these individuals forgo their own reproduction and help another reproduce? This question troubled even Darwin, who speculated that selection may act on the entire colony rather than on individuals alone.

Vero C. Wynne-Edwards proposed that cooperation may result from **group selection**, or selection acting on groups (Wynne-Edwards 1962). Exploring why animals do not overexploit resources, he suggested that they can regulate breeding and population size by defending widely spaced territories or establishing dominance hierarchies in which only the most dominant individuals—those that successfully establish a territory—reproduce. If all individuals attempted to maximize their fitness by reproducing, he reasoned, resources would be overexploited, leading to extinction (Applying the Concepts 3.1).

### APPLYING THE CONCEPTS 3.1

#### Do lemmings commit suicide?

Biologists critically evaluate group selection, but you might get a very different impression from documentaries and television that commonly use group selection to explain behavior. One classic example of group selection thinking is the myth that lemmings commit suicide to prevent overpopulation. This myth was popularized in a 1958 Disney documentary, *White Wilderness*, about animals living in the Arctic. Lemmings are small, herbivorous rodents common in this area (Figure 1) and display drastic changes in population sizes approximately every four years (Chitty 1996). When population density increases, lemmings and many other animals disperse to find new, less populated habitats. In one memorable scene in the documentary, lemmings appear to commit suicide by jumping off a cliff into the Arctic Ocean and swim off to their death, presumably to prevent overpopulation and the exhaustion of resources.

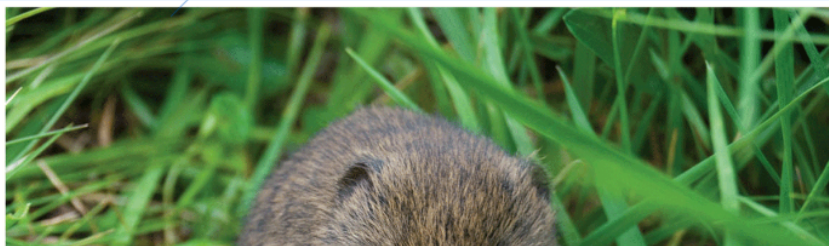


FIGURE 1. A lemming.

However, there is no evidence that individuals deliberately commit suicide. Such an explanation, in fact, runs up against problems with the logic of group selection. Individuals that did not cooperate in committing suicide would have higher fitness than those that did, and “cheating” individuals would quickly come to dominate the population. In reality, lemmings are simply dispersing to reduce intra-specific competition. The dramatic “suicide” in the movie was actually staged for the camera (Chitty 1996). ■

#### Video: Excerpt from Lemming Drop

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Video: Excerpt from Lemming Drop



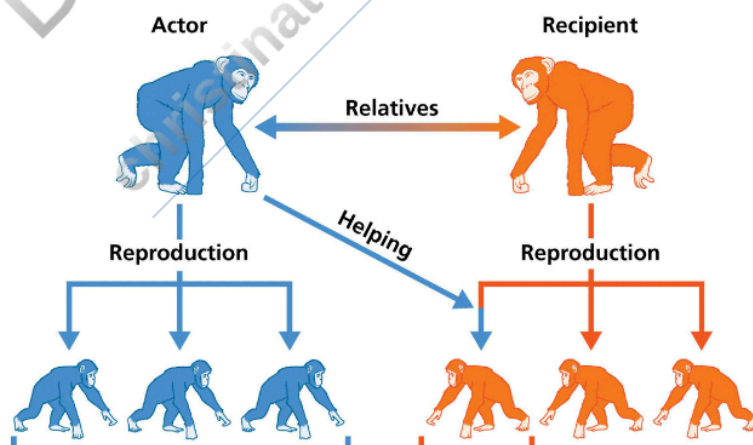
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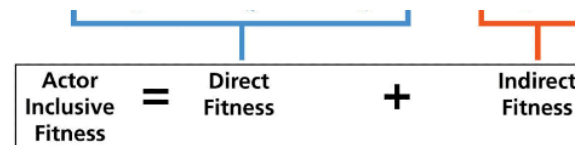
Find out more

Group selection quickly gained popularity as a way to explain cooperative behavior and is still commonly invoked by nonscientists, but does it explain why individuals cooperate? George Williams said no (Williams 1966). Territoriality does not need to be the result of a group's efforts to limit the use of resources; individuals may simply compete for available resources. In fact, Williams argued, group selection is based on faulty logic. An individual that did not limit its reproduction (a "cheater") would have a fitness advantage. The offspring of "cheaters" would quickly become a larger and larger portion of the population until none of the individuals exhibited cooperative behavior.

At about the same time, William Hamilton proposed a new explanation for why animals engage in cooperative behavior. He argued that the total fitness of an individual actor (its genetic contribution to the next generation) comprised both direct and indirect components. **Direct fitness** is determined by the number of offspring produced by the actor, due to its own behavior in the absence of help by others, while **indirect fitness** is determined by the offspring of relatives that exist because of the actor's cooperative behavior. Together, direct and indirect fitness make up **inclusive fitness** (Figure 3.17).



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**FIGURE 3.17. Inclusive fitness.** Inclusive fitness of an actor is the sum of direct and indirect fitness. Indirect fitness does not include all of the reproductive success of relatives (orange offspring), only that which is due to the behavior of the actor (helping arrow). (Source: West, Griffin, & Gardner 2007)

Hamilton's idea has come to be known as **kin selection**, a process in which an individual can increase its total fitness by helping kin, because they share genes from a common ancestor (Hamilton 1964; Maynard Smith 1964). In other words, an individual can increase its genetic contribution to the next generation by helping close relatives that share alleles through common descent, a situation found in many social insect colonies. Hamilton's insight has had a profound influence on our understanding of behavior. (We examine cooperation and kin selection in much more detail in Chapter 16.)

Not everyone was ready to dismiss group selection, however. For one thing, not all cooperating social insects display a close genetic relationship among workers, often because two or more queens produce offspring (e.g., Kümmerli & Keller 2007). In response, David Sloan Wilson and others developed a new model of group selection. They argue that **multilevel selection**, selection on groups, may be stronger than selection on individuals in certain restrictive circumstances: groups must be small, and there must be minimal movement of individuals between groups (e.g., Wilson & Wilson 2007). Theoretical models show how multilevel selection can operate (Marshall 2011; Simon & Nielsen 2012; Lehtonen 2016), yet empirical support is sparse (but see Pollock, Cabrales, Rissing, & Binmore 2012) and so debate about the importance of multilevel selection for understanding the evolution of cooperation continues (Liao, Rong, & Queller 2015; Nowak & Allen 2015; Kramer & Meunier 2016). However, kin selection and multilevel selection need not be mutually exclusive: both can affect the evolution of behavior within a species (Biemaskie & Foster 2016).

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### 3.4 Sexual selection is a form of natural selection that focuses on the reproductive fitness of individuals

#### Learning Objectives

After reading this section, you should be able to

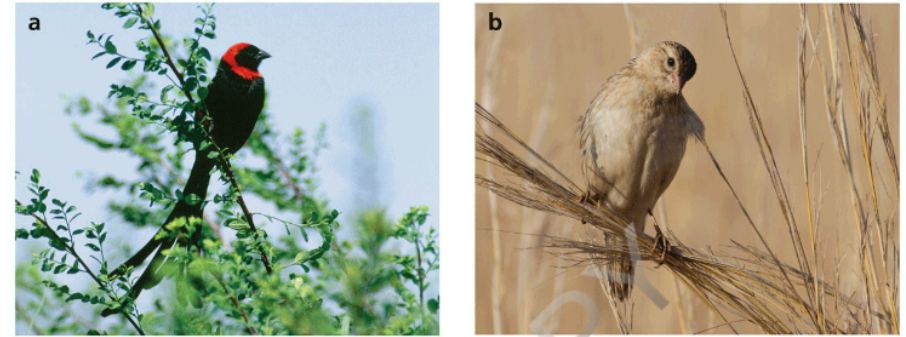
- distinguish between sexual and natural selection and
- identify an example of sexual dimorphism.

Natural selection acts on heritable traits that affect survivorship and reproduction. **Sexual selection** is a form of natural selection that acts on heritable traits that affect reproduction. Individuals vary in their ability to compete for mates or attract individuals of the opposite sex, which leads to differential reproduction within a sex.

Darwin proposed that many traits observed in males and females of a species are due to sexual selection and often result in **sexual dimorphism**, or morphological differences between the sexes. Which traits are involved in sexual selection? Let's consider the case of widowbirds.

#### FEATURED RESEARCH Sexual selection in widowbirds

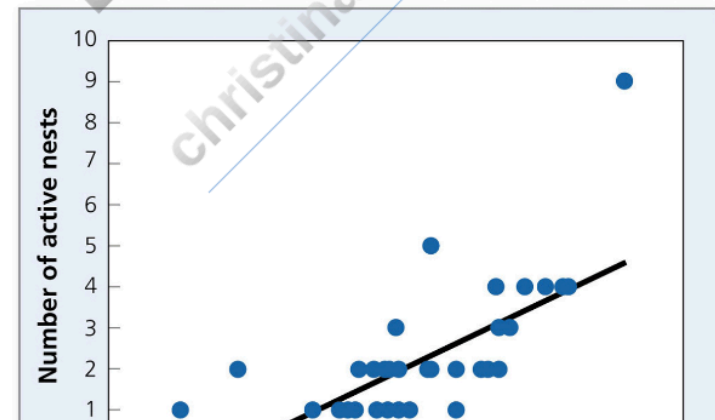
Widowbirds are medium-sized birds found in Africa that often display sexual dimorphism in both color and tail length. Red-collared widowbird (*Euplectes ardens*) females have brown plumage and short tails, while males have black plumage with a bright red collar around their head and extremely long tails ([Figure 3.18](#)). In this species, males establish and defend large territories that females visit at the start of the breeding season. When a female is present, the male performs an elaborate courtship flight in which the tail is prominently displayed. Females visit the territories of several males before selecting one with which to mate, build a nest, and raise offspring. Multiple females can breed in a single male territory.

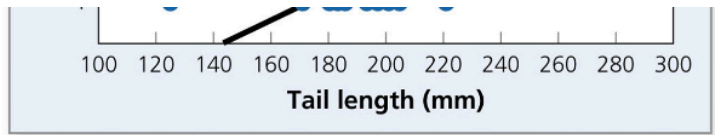


**FIGURE 3.18.** Red-collared widowbirds. (a) Males have extremely long tails and brighter plumage. (b) Females lack these traits.

Sarah Pryke, Staffan Andersson, and Michael Lawes investigated whether sexual selection through female choice could explain the evolution of dramatic coloration and long tails in males ([Pryke, Andersson, & Lawes 2001](#)). They examined the traits of the males that females preferred to mate with: Were they those males that had the longest tails or those that had the largest color patches? Prior to the start of the breeding season, the research team captured 43 males from a population in South Africa, placed a unique color band on their leg for identification, measured their tail length and color patch size, and released them. Males were then observed daily both to estimate their territory size and to determine the number of females that nested within each male's territory (his mating success).

The team found that there was variation in male tail length (12–28 cm), color patch size, territory size, and the number of females breeding within a single male's territory (0–9). Pryke and her colleagues determined that male mating success was most strongly and positively correlated with the male's tail length ([Figure 3.19](#)) but not with his territory size or color patch.





**FIGURE 3.19. Male widowbird mating success.** Males with the longest tails had the highest mating success.

In this population, females appear to preferentially mate with males possessing the longest tails. Such mate choice by females can help to explain the evolution of sexually dimorphic tail length in this species. Because

long tails likely are energetically costly (both to produce and in terms of flight costs), only those males in the best condition—the highest-quality males in the population—can survive, defend a territory, and display actively to females. If male phenotype (e.g., tail length and overall genetic quality) is heritable, females can enhance the fitness of their offspring by mating with such males. Pryke and colleagues' data, however, cannot explain the evolution of bright color in males by female choice. The researchers suggest that male coloration might play a role in male–male competition for territories, but this hypothesis requires further evaluation.

Sexual selection is an important force that can produce wide variation in reproductive success and fitness among individuals, and affect the evolution of traits. As we will see in [Chapter 12](#), sexual selection is an area of great activity in behavior research.



## CHAPTER REVIEW

### 3.1 Evolution by natural selection favors behavioral adaptations that enhance fitness

- Individuals in populations vary in the traits they possess.
- Individual's different traits are at least partly heritable.
- Traits confer differences in survivorship and reproduction.
- Adaptations are heritable traits of individuals in populations that evolve through the process of natural selection.
- Heritability can be quantified through parent-offspring regression and selection experiments.
- The fitness of a trait may depend on its frequency in a population.

### 3.2 Modes of natural selection describe population changes

- The frequency of traits in populations will change over time via directional, stabilizing, and disruptive selection.

### 3.3 Individual and group selection have been used to explain cooperation

- Natural selection will most often act on individuals based on how their traits influence their ability to survive and reproduce.
- In some circumstances, selection may act more strongly on groups than on individuals.

### 3.4 Sexual selection is a form of natural selection that focuses on the reproductive fitness of individuals

- Sexual selection acts on traits that affect reproduction.
- Sexual selection can explain the evolution of sexual dimorphic traits.

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## CHAPTER 2

# Methods for Studying Animal Behavior

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

- 2.1 [Animal behavior scientists generate and test hypotheses to answer research questions about behavior](#)
- 2.2 [Researchers use observational, experimental, and comparative methods to study behavior](#)
- 2.3 [Animal behavior research requires ethical animal use](#)
- 2.4 [Scientific knowledge is generated and communicated to the scientific community via peer-reviewed research](#)

### Features

- |                        |   |
|------------------------|---|
| Scientific Process     | 2.1 <a href="#">Jumping tadpoles</a>  |
| Applying the Concepts  | 2.1 <a href="#">Project Seahorse</a>  |
| Toolbox                | 2.1 <a href="#">Animal sampling techniques</a><br>2.2 <a href="#">Scientific literacy</a> |
| Quantitative Reasoning | 2.1 <a href="#">Sampling methods</a>  |

When we were graduate students, we quickly learned that research does not always go as planned. During a study of the mating behavior of round stingrays (*Urolophus halleri*) in the Gulf of California, observations ended abruptly after a large storm created adverse conditions and all the stingrays left the study area. Luckily, they returned after a few days when the weather stabilized and we were able to continue the research (Nordell 1994).

returned after a few days when the weather stabilized and we were able to continue the research (Nordell 1994).

Many research projects begin with detailed planning. Yet scientific research sometimes begins almost as an “Aha!” moment, as it did for ecologist Stephen Yanoviak (2006). It all started during a project to study deforestation and the spread of mosquito-borne tropical diseases in Peru. Yanoviak was collecting mosquitoes in the rainforest canopy 30 m (over 100 ft) off the ground when he was attacked by ants. He noticed that, after he brushed some of the ants off his body, they did not fall to the ground but appeared to glide back to the tree trunk, as if they could somehow direct their movement. Later, he collaborated with Michael Kaspari and Robert Dudley to examine this behavior more thoroughly. They found that about 85% of the individuals in the ant species *Cephalotes atratus* seemed to be able to direct their gliding flight behavior (Yanoviak, Dudley, & Kaspari 2005) (Figure 2.1). This was an exciting finding, as no one had known that ants possessed this ability. In this case, scientific discovery began quickly and accidentally.



**FIGURE 2.1.** *Cephalotes* ant. This species of ant can direct its gliding behavior, as ecologist Stephen Yanoviak discovered.

In this chapter we begin by exploring how scientists generate and test hypotheses to answer research questions about animal behavior. We then discuss how animal behavior researchers collect data using observational, experimental, and comparative research methods. Essentially, we examine the nuts and bolts of how animal behavior research is conducted. Next, we discuss important ethical issues in the study of animal behavior. We close the chapter by looking at how scientific knowledge is generated and communicated to the scientific community through peer-reviewed research.

### Video: Gliding ants

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In this chapter we begin by exploring how scientists generate and test hypotheses to answer research questions about animal behavior. We then discuss how animal behavior researchers collect data using observational, experimental, and comparative research methods. Essentially, we examine the nuts and bolts of how animal behavior research is conducted. Next, we discuss important ethical issues in the study of animal behavior. We close the chapter by looking at how scientific knowledge is generated and communicated to the scientific community through peer-reviewed research.

### Video: Gliding ants

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## Canopy Arthropod Biology

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## 2.1 Animal behavior scientists generate and test hypotheses to answer research questions about behavior

## Learning Objectives

After reading this section, you should be able to

- explain how hypotheses can be generated and tested, as Uetz and his colleagues demonstrated in research studies on brush-legged wolf spiders;
- describe how Lima and his colleagues used a model to generate hypotheses and test predictions from that model; and
- generate a research question and testable hypothesis.

To study the behavior of animals, scientists must form and test hypotheses to answer research questions. These questions can be based on earlier observations, previous knowledge, prior research, a theory, or some combination of these. Let's examine how this process works using the case of wolf spiders.



**FIGURE 2.2.** Wolf spider. Male brush-legged wolf spiders wave and tap their forelegs to court females.

## FEATURED RESEARCH Hypothesis testing in wolf spiders

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The brush-legged wolf spider (*Schizocosa ocreata*) is common in the leaf litter habitat of eastern North American forests. During the brief breeding season each spring, males search for females (Figure 2.2). Females typically mate only once, whereas males mate multiple times; unmated females thus become increasingly rare as the breeding season progresses. How do males find unmated females? Females are cryptic, meaning that their coloration lets them blend in well with the leaf litter, and they may often be hidden from the view of a male. As a result, males search for females slowly, using chemical cues that females deposit on silk threads in the leaf litter. When males find receptive females, they court them with a multimodal display by walking rapidly in a jerky fashion while waving and tapping their forelegs (providing visual cues). They also transmit vibrations through the substrate by rubbing specialized organs together (providing seismic cues). These signals can be sensed by the female and may also be used by other nearby males as a cue to the presence of a potential mate.

## Video: Male brush-legged wolf spider doing jerky tap courtship behavior

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Video: Male brush-legged wolf spider doing jerky tap courtship behavior

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George Uetz and collaborators from his lab, Andy Roberts and Phil Taylor, were interested in this mating behavior (Roberts et al. 2006). They investigated the following research hypothesis:

**Research hypothesis:** Male wolf spiders use the behavior of nearby males to find receptive females.

The null hypothesis is that males do not use the presence and behavior of other males as a cue to locate receptive females, while the alternate hypothesis is that they do. The alternate hypothesis predicts that the presence and behavior of a rival male will cause the searching male to move in the rival's direction, search for a female, and begin courtship tapping.

The research team tested these predictions by conducting an experiment. They collected juvenile spiders from a nearby forest and raised them in the lab until they were sexually mature. Focal males (the subjects of study) were tested for their reactions to (1) visual cues only (the sight of a demonstrator male tapping), (2) seismic cues only (the vibrations of another male tapping), and (3) both cues simultaneously. The researchers prompted the demonstrator males to tap by providing them with the silk of females that contained their chemical cues. They recorded the focal male's behavior for three minutes prior to the stimulus, three minutes during, and three minutes after. This approach allowed researchers to characterize baseline behavior and examine changes in behavior after exposure to test stimuli. In each phase of a trial, the research team recorded two behaviors: chemoexplore behavior, exploratory mate searching behavior to detect chemical signals (slow walking while rubbing the substrate with the pedipalp), and jerky tap behavior, courtship behavior to attract a mate (rapid walking in jerky movements while tapping the substrate).

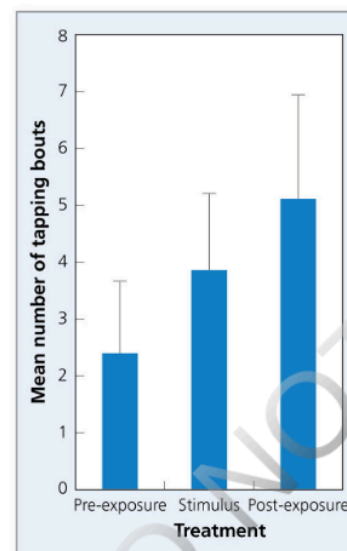
The researchers used 15 focal males in each treatment. In any study, it is important to collect data on many individuals to ensure that data are representative of the population or species. Individuals always exhibit variation, but some may exhibit particularly unusual behavior, perhaps as a result of hunger or disease. The collection of data from many individuals helps prevent researchers from drawing conclusions that are based on only a few nonrepresentative individuals.

The research team found that the treatments had no effect on chemoexplore or jerky tap behavior. From these data, the team accepted the null hypothesis: male wolf spiders do not appear to use the visual or vibratory behavior of a courting rival as a cue to the location of a receptive female. Apparently, males just have to find females on their own.

Then a funny thing happened. A year or so later, Uetz, Roberts, and Dave Clark were examining the mating behavior of these spiders in the wild and observed males heading in the direction of other males that were tapping in courtship. This behavior was exactly what they did *not* observe in their lab experiments. What was going on? They remembered that, in their previous experiment, they had used a population of males raised in isolation in captivity that had no experience with rival males. Could prior social interactions be an important prerequisite for this behavior?

To test this new idea, the researchers conducted similar experiments using adult males caught in the wild. This

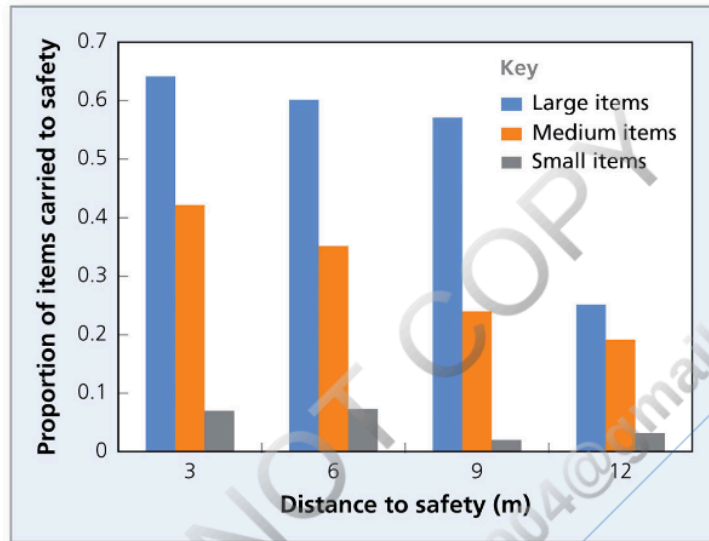
time, they found that the focal males did display a greater frequency and duration of interactive behaviors (i.e., approach, follow, and watch) when exposed to a courting male (another male tapping). They also displayed more bouts of courtship activity during and after the presentation of another courting male (Figure 2.3). These findings indicated that male wolf spiders can indeed use the tapping of rival males as a cue for finding females (Clark, Roberts, & Uetz 2012).



**FIGURE 2.3. Male courtship behavior.** Mean (+ SE) tapping bouts during a three-minute trial for each of the three treatments. (Source: Clark, Roberts, & Uetz 2012)

This story illustrates an important point about how science progresses. Research is an ongoing process of discovery. The behavior of males in the wild did not seem to match observations of laboratory-reared subjects, which led to a new hypothesis and experiments and a new understanding of spider behavior.

food-carrying behavior they observed in gray squirrels indeed represents a behavioral trade-off between maximizing energy intake rate and minimizing predation risk.



**FIGURE 2.7. Food-carrying behavior.** The proportion of large (blue), medium (orange), and small (gray) food items carried to safety for consumption. (Source: [Lima, Valone, & Caraco 1985](#))

In fact, many species carry food to a safe location before eating it, and other experiments have demonstrated a similar behavioral trade-off in many species of birds ([Lima 1985](#); [Valone & Lima 1987](#)). For example, black-capped chickadees (*Parus atricapillus*), blue jays (*Cyanocitta cristata*), and white-throated sparrows (*Zonotrichia albicollis*) behaved just like squirrels in various tests. Other species, such as cactus wrens (*Campylorhynchus brunneicapillus*) and eastern towhees (*Pipilo erythrophthalmus*), carried more of the large than the small items but did not carry more items when close to safety. Finally, the carrying behavior of house finches (*Carpodacus mexicanus*) was completely inconsistent with both predictions of the model. We don't know why the model doesn't work for all species, but one possibility is that species perceive predation risk in different ways—maybe this could serve as a research project for you.

It is clear from the examples here that hypotheses make testable predictions about behavior. Next, we turn our attention to the different methods used to study behavior and test predictions.

## 2.2 Researchers use observational, experimental, and comparative methods to study behavior

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### Learning Objectives

After reading this section, you should be able to

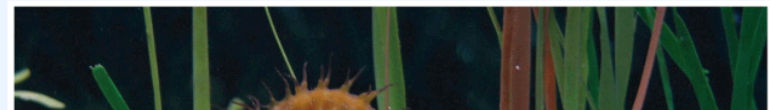
- define each of the three general methodological approaches used to study animal behavior,
- describe how Pelletier's research on foraging and mating tactics of bighorn sheep demonstrates the use of the observational method,
- describe how de Sousa's research on predators and tadpole jumping utilized the experimental method, and
- describe how Weber and Hoekstra's research on the evolution of burrowing behavior in several mice species utilized the comparative method.

When conducting research, scientists must determine the best method to address their research questions and test their hypotheses. Three common methods used in behavioral research are the observational, experimental, and comparative methods ([Altmann 1974](#); [Lehner 1998](#); [Bateson & Martin 2007](#)). It is important to note that numerous protocols or data collection techniques can be used with each method and that researchers often employ more than one method in their studies ([Applying the Concepts 2.1](#)). In addition, data must be analyzed to see if the patterns observed support the prediction.

### APPLYING THE CONCEPTS 2.1

#### Project Seahorse

Amanda Vincent began studying seahorses because she wanted to conduct research outdoors and in the sea. Later, she became fascinated with the animal, particularly its unusual reproductive behavior: for example, only male seahorses get pregnant ([Figure 1](#)). Vincent's work involved spending many hours conducting observations. Seahorses had rarely been observed in the wild, and very little was known about their behavior. Her research began with basic questions about seahorse mating behavior: Are they monogamous? What are the behavioral differences between the two sexes? Do males defend territories? To answer these questions, Vincent had to find the seahorses during their reproductive periods. These animals can be very cryptic and blend into their environment. She also had to develop techniques for tagging individuals so she could identify them later and design appropriate measures of behavior.



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**FIGURE 1. Seahorse.** This pregnant male big-belly seahorse (*Hippocampus abdominalis*) is one of many seahorse species studied by Dr. Vincent. It is found only along the coasts of Australia and New Zealand.

Because of the research conducted by Vincent, her students, and colleagues, we now know much more about the unique behaviors of seahorses. It turns out that some species are truly monogamous, which is very rare in the animal world and even rarer among fish. Experiments Vincent conducted have demonstrated that mated pairs greet each other in a daily ritual that appears to be important in maintaining that monogamous bond (Vincent 1995a). In addition, her research indicates that many populations of seahorses and pipefish are decreasing because they are heavily harvested for Chinese medicine, curios, and the hobby aquarium market (Vincent 1995b). In response, Vincent and Heather Koldewey founded Project Seahorse to protect seahorse populations while ensuring sustainable livelihoods for those dependent on seahorse fishing. Vincent continues to both study seahorses' behavior (e.g., Vincent, Evans, & Marsden 2005) and work for their conservation (e.g., Vincent 2008). For more information, see the Project Seahorse website. ■

#### Video: Why are seahorses under threat?

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## The observational method

In the **observational method**, scientists observe and record the behavior of an organism without manipulating the environment or the animal. This method is commonly used both to test hypotheses and to describe behavioral patterns. For example, it is used to construct ethograms, as we saw in Chapter 1. Researchers studying animals in zoological parks frequently use the observational method to examine activity patterns because behavior is often an important indicator of well-being or level of stress (Hill and Broom 2009). For instance, changes in the behavior of an animal may indicate changes in its reproductive condition or health (Wittmaack et al. 2015) or the effects of exhibit design on animal stress levels (Fernandez et al. 2009, Rose et al. 2018). Researchers studying animals in the wild also use the observational method to test hypotheses, as we see next.

## FEATURED RESEARCH The observational method and male mating tactics in bighorn sheep



Fanie Pelletier observed bighorn sheep (*Ovis canadensis*) (Figure 2.8) in a large provincial park in Canada to examine how male mating tactics affect the time they could spend foraging (Pelletier 2004). During the rutting (mating) season, males exhibit two distinct mating strategies. Dominant (tending) males guard a single estrous ewe from competitors, to keep them from also mating with her. Such guarding behavior often involves head-butting fights with other males. Subordinate (coursing) males will attempt to chase estrous ewes to separate them from a dominant male and then try to mate with a separated ewe. Pelletier asked whether the tending behavior used by dominants constrained their foraging time more than the coursing behavior used by subordinates; she predicted that tending would be more time consuming and thus constrain foraging behavior more than coursing.



**FIGURE 2.8.** Bighorn sheep. A dominant male tending a female.

Pelletier observed rams in a marked population in which all individuals were uniquely marked as lambs. She collected behavioral data during the rutting season (November–December). During this time, males frequently switch groups and can change from tending to coursing if a more dominant ram joins a group. Because the groups are more dynamic and more dispersed, it was not possible to monitor more than one ram at a time. Therefore, she recorded the time when individual focal animals transitioned from one behavior to another in three to six one-hour focal observation periods each day of the rut (averaging 28 hours of observation for each male for the pre-rut and 27 hours during the rut). She then calculated the amount of time spent in each behavior (Toolbox 2.1).

### TOOLBOX 2.1

#### Animal sampling techniques

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As mentioned earlier, Fanie Pelletier (2004) used continuous focal-animal observations to collect data on bighorn ram behavior in the pre-rutting season. In this technique, the researcher records all behaviors for focal animal(s) over a given period, thus providing a complete record of the behavior observed. During this period, the researcher often records the frequency, duration, or latency (time until initiation) of behaviors.

While continuous focal-animal observations provide complete data, they require the ability to observe specific individuals continuously for long periods of time. More commonly, researchers use **focal animal sampling**, as Pelletier did during the sheep's rutting season. In this technique, researchers collect snapshots of behavior using standardized sampling techniques, where a focal individual is randomly selected and observed for a specified period, and all pertinent behaviors performed by the individual are recorded (Altmann 1974). After the time has expired, a different individual is randomly selected and observed. Focal animal sampling has several advantages:

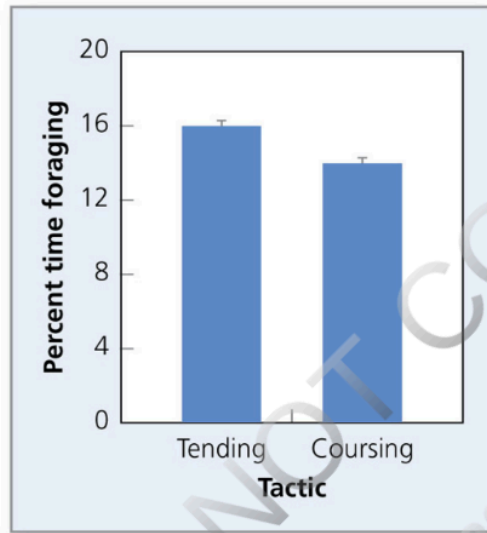
1. The behavior of different individuals is sampled. If individuals have unique markings or morphological aspects, the researcher can record the behavior of known individuals and identify the total number of unique individuals sampled. If it is difficult to identify individuals, the researcher can move to a different location before selecting a new individual. The researcher can also simply select an individual that is some distance away from the last focal animal observed. This ensures that a number of different individuals are sampled.
2. Because random individuals—not individuals that exhibit either unusually high or low levels of a particular behavior—are selected, sampling is unbiased.
3. Because data are collected over a recorded amount of time, researchers can easily calculate the frequency of a behavior and the rate at which the behavior was displayed.
4. This technique requires little more than being able to keep track of time and observe and record behavior. Depending on the situation, these tasks might best be accomplished by a pair of researchers: a recorder, who keeps track of time and records the behavior, and an observer, who watches the animal and describes the behaviors displayed.

Another common sampling technique is known as **instantaneous** or **scan sampling**. Here, data are collected from individuals at regular time intervals. For instance, you might be interested in the frequency with which individuals in a group scan their environment (i.e., raise their head to observe their surroundings). You could use scan sampling at 30-second intervals to record the number of group members whose head is raised at a given moment. Over a sufficiently long observation period, these data would provide information on the percentage of time individuals spend scanning the environment. Altmann (1974) provides details of these and other sampling methods.

There was a great deal of individual variation in time spent foraging, ranging from 10% to 77%, and adult males foraged less during the rutting season than during the pre-rut. However, there was no significant difference in the proportion of time spent foraging by males when tending or coursing during the rut (Figure 2.9). Pelletier's results, then, did not support her prediction: tending males did not forage less than coursing males. Why might this be? One possibility is that tending males don't have to spend time chasing females and can actually spend time

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be? One possibility is that tending males don't have to spend time chasing females and can actually spend time feeding, even as they guard a ewe. These animals live in mountainous areas, which may enable a ram to position himself on a rocky cliff in a way that makes it difficult for other males to approach the defended ewe, allowing more time to feed.



**FIGURE 2.9. Bighorn sheep foraging time.** Mean (+ SE) proportion of time spent foraging by bighorn rams while tending or coursing during the rut. (Source: [Pelletier 2004](#))

## The experimental method

In the **experimental method**, scientists manipulate or change a variable to examine how it affects the behavior of an animal. The variable that is changed—the independent variable—can be anything that we measure, control, or manipulate. It can be abiotic (e.g., temperature, humidity, wind) or biotic (e.g., habitat, food availability, social interactions). The researcher then measures changes in another variable, the dependent variable, that occur in response to changes in the independent variable. If you were examining how food availability affects clutch size (the number of eggs laid by a female during one reproductive attempt), your experimental treatment might consist of manipulating the amount of food (the independent variable) and then measuring the number of eggs produced (the dependent variable).

To determine whether your manipulation is actually influencing the dependent variable, it is essential to include a **control group**, which does not experience the manipulation but is treated similarly in all other aspects. In the simplest experimental design, only one factor differs between the experimental and control groups. In essence, the control group represents the null hypothesis, and the experimental group represents the alternate hypothesis.

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## FEATURED RESEARCH The experimental method and jumping tadpoles

Verônica de Sousa and her colleagues used the experimental method to study an unusual behavior of an undescribed species of tropical tadpole (*Pseudopaludicola* sp.) ([De Sousa, Teresa, & de Cerqueira Rossa-Feres 2011](#)). *Pseudopaludicola* are very small frogs (less than 20 mm snout–vent length) found throughout South America ([Laufer & Barreneche 2008](#)). During the rainy season, females lay eggs in the small puddles formed from the footprints of large mammals at the edge of ponds and swamps. The eggs develop into tadpoles that go through metamorphosis in these small puddles. Also in these puddles are aquatic juvenile dragonflies (naiads), voracious predators of tadpoles, fish, and invertebrates.

The researchers observed that tadpoles sometimes jump out of their puddles and wondered why they exhibit this behavior. One possibility is that they are attempting to escape from predators. The puddles tend to be closely spaced and numerous, so a tadpole might be able to jump to a safer one. The team examined two questions: (1) Is tadpole jumping behavior a response to the presence of a predator? and (2) Does the jumping behavior increase survival ([Scientific Process 2.1](#))?

### SCIENTIFIC PROCESS 2.1

#### Jumping tadpoles

Research Question: *Why do tadpoles jump out of puddles?*

#### Hypothesis:

Jumping is an antipredator behavior.

#### Prediction:

Tadpoles will jump most often from puddles that contain a predator.

#### Methods:

The researchers:

- Collected tadpoles and dragonfly naiad predators from the field
- Acclimated tadpoles in individual aquaria in the lab for four to five days
- Created experimental arenas with sandy bottoms to simulate puddles (9 cm diameter, 4.5 cm depth)

#### Experiment 1:

41 tadpoles each experienced three treatments:

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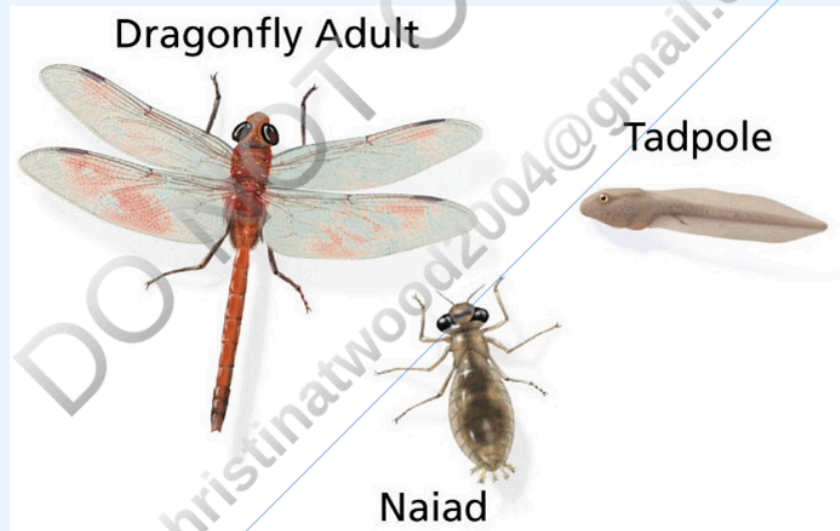
72 tadpoles each experienced three treatments.

1. **Predator treatment (PRE):** one naiad in the arena.
2. **Predator control treatment (CPRE):** an inanimate object (similar in size to a naiad) in the arena to control for the presence of a novel object.
3. **Control (CON):** no object or predator in the arena.

Each trial lasted 45 minutes and was videotaped. Researchers recorded jumping behavior (number of jumps).

#### Results:

Jumping behavior was most common in the predator-present (PRE) treatment.



**FIGURE 1.** Predators and prey. Juvenile dragonflies (naiads) feed on tadpoles. Adult dragonflies are much larger than naiads.

#### Experiment 2:

21 tadpoles were randomly assigned to one of two predator treatments:

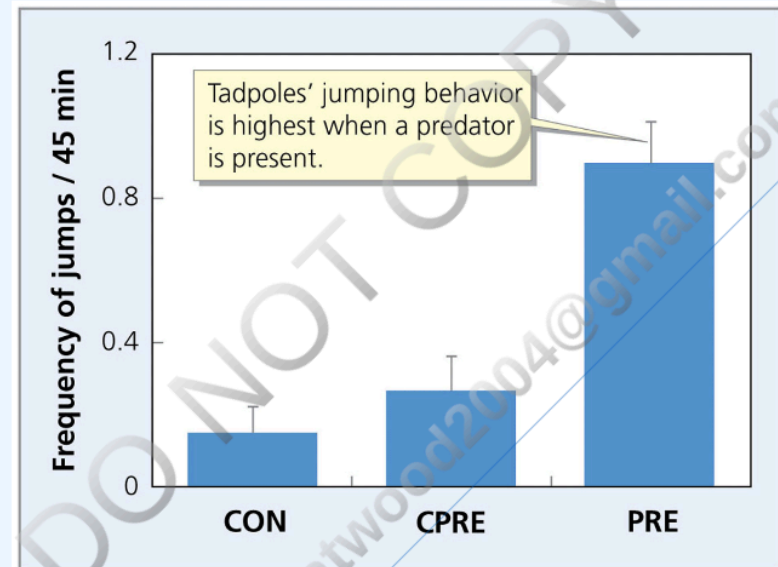
1. **Screen treatment:** a screen was placed over the arena to prevent the tadpole from jumping out.

2. **Nonscreened treatment:** no screen was placed over the arena, allowing the tadpole to jump out.

Each trial lasted three hours or ended when the tadpole was consumed.

#### Results:

Survival was highest in the nonscreened arena treatment.



**FIGURE 2.** Jumping behavior. The mean (+ SE) frequency of jumping was higher for the predator treatment than for both controls. (Source: [de Sousa, Teresa, & de Cerqueira Rossa-Feres 2011](#))

#### Conclusion:

Tadpole jumping behavior is an effective antipredator behavior that enhances survivorship.

#### Evaluate

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Explain the advantage of using two different controls in this experiment.

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The researchers collected tadpoles and dragonfly naiads and created small experimental arenas to simulate puddles. To examine the effect of a predator on jumping behavior, they conducted an experiment with three treatments that differed in the presence or absence of the naiad predator and then measured the frequency of tadpole jumping. They found that the frequency of tadpole jumping was significantly higher in the predator-present treatment than in either control treatment. Most jumps occurred in response to naiad movement.

To examine how jumping behavior affects tadpole survival, they conducted another experiment with tadpoles and naiads, using two treatments that differed in whether tadpoles could get away from the predator. For this experiment, they measured the number of tadpoles that survived and found that the survival rate was much higher in the treatment in which tadpoles could escape the predator.

These experimental results indicate that naiad predators kill tadpoles and that tadpole jumping is an effective antipredator behavior that may have significant fitness benefits. Since tadpoles are aquatic, wouldn't jumping out of the puddle cause them to desiccate? Observations in the field confirm that tadpoles do spend quite a bit of time out of puddles, and yet they survive. There is often a thin film of water on the substrate that likely reduces the risk of desiccation.

This research study illustrates a strength of the experimental method: specific factors are manipulated to examine their effect on behavior. However, such control often requires research to be conducted in an artificial setting (i.e.,

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laboratory), which may affect behavior. Another aspect of experimental studies is that they often require greater financial and logistical support than observational studies.

Finally, we examine a third method used to study behavior, particularly how behaviors evolve.

### Video: Tadpole control

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### Video: Tadpole predator control

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### Video: Tadpole predator treatment

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The patterns in the behavioral studies and the phylogeny provided information about the evolution of burrowing behavior in these species. The analysis indicated that the ancestral trait is the absence of burrowing and that the construction of large, complex burrows is a derived trait. They also found that sister species often exhibited significant differences in burrowing behavior. For example, *P. polionotus* frequently burrows and builds long complex burrows while its sister species, *P. maniculatus*, burrows less frequently and builds rather simple short burrows. Two species that do display similar burrowing frequency, length, and complexity of burrows, *P. polionotus* and *P. aztecus*, are not each other's closest relatives. Because burrowing behavior was so varied among these closely related species, the researchers concluded that variation in this behavior most likely evolved independently in the different species. These conclusions are supported by more recent work that indicates a genetic basis for burrowing behavior in these mice ([Weber, Peterson, & Hoekstra 2013](#)).

As we've just seen, animal behavior can be examined using a variety of methods. Next, we examine how the study of animal behavior requires careful attention to ethical animal use.

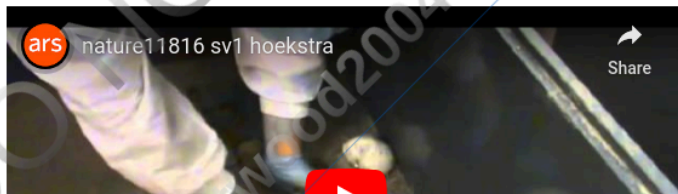
### Video: Making burrow casts

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## 2.3 Animal behavior research requires ethical animal use

### Learning Objectives

After reading this section, you should be able to

- describe the 3Rs and
- explain how the 3Rs relate to the ethics of animal care research.

In the previous chapter, we examined the process of science as being fundamental to understanding the natural world. That said, scientists are not infallible. We will now look at two ethical issues related to the study of animals: scientific misconduct and animal care.

**Scientific misconduct** includes the falsification or fabrication of data, purposefully inappropriate analysis of data, and plagiarism. Misconduct can occur in all branches of science and can be identified by other researchers. If a problematic paper is published, misconduct is typically identified when other scientists cannot successfully replicate the findings.

Researchers studying animals must also consider how their work affects the individuals they study. The better we understand the behavior of animals, the better we can manage and care for them ([Rose et al. 2017](#)). However, research can also have negative impacts on animals. These can arise from simple observations of wild animals, inappropriate housing of animals in laboratories, and the various procedures performed. Scientists and governments have therefore developed ethical standards for animal research.

### How research can affect animals

Observing animals in their natural environment often involves the lowest level of invasiveness and stress for individuals. However, even observational field research can negatively affect the animals studied. For example, repeatedly observing individuals can habituate them to humans. If individuals lose their fear of humans, they can become subject to increased predation from poachers or hunters. Manipulations of the animal's environment, such as providing supplemental food, can lead to other unintended consequences. A large addition of food could result in a substantial increase in the population, which might result in overcrowding and increased stress ([Robb et al. 2008](#)).

Other kinds of behavioral research require more direct contact with animals. For example, field researchers may need to collect blood or tissue samples, quantify parasite loads, measure reproductive condition or morphology, or uniquely mark individuals. These procedures can increase animals' stress levels because researchers must trap, restrain, or anaesthetize individuals. Animals in captivity require additional considerations ([Figure 2.11](#)), including appropriate housing and husbandry (feeding and care) ([Grandin 2010](#)) and how the animals will be procured. Researchers also need to determine the fate of the animals when the research is completed. Some animals may have to be sacrificed for examination of their body organs. For example, researchers studying how mating behavior affects neurobiology may need to examine the brains of their study organisms (e.g., [Huang & Hessler 2008](#)).





**FIGURE 2.11.** Animal care. A zoo veterinarian examines a sea lion.

## Sources of ethical standards

Most nations have set guidelines for the use of animals in research and teaching. In the United States, a variety of federal agencies and organizations have formulated specific guidelines that scientists must follow to maintain their funding. These include the National Institutes of Health Office of Animal Care and Use, the Department of Agriculture Animal and Plant Health Inspection Service, the Association for the Assessment and Accreditation of Laboratory Animal Care, and the American Association for Laboratory Animal Science. In Canada, the Canadian Council on Animal Care sets these standards, while in Europe they come from the Council of Europe Conventions on the Protection of Animals and the European Biomedical Research Association.

Scientific societies also have animal care guidelines. These include the guidelines established by the Animal Behavior Society and its UK counterpart, the Association for the Study of [Animal Behavior \(2006\)](#), the American Society of Mammalogists ([Sikes et al. 2011](#)), the American Fisheries Society (2013), the Ornithological Council (2010), and the American Society of Ichthyologists and Herpetologists (2004). In addition, the National Research Council's Institute of Laboratory Animal Research Commission on Life Sciences publishes a free online book on animal care ([Institute for Laboratory Animal Research 2010](#)).

## The three Rs

Although there are differences among guidelines in different countries, most follow the 3 Rs: replacement

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Although there are differences among guidelines in different countries, most follow the 3 Rs: replacement, reduction, and refinement. **Replacement** means using computer modeling, videotapes, or other approaches in place of actual animals. **Reduction** refers to limiting the number of animals subject to disturbance in research or teaching. Such an effort requires much thought and perhaps pilot studies in order to design a study that uses the fewest possible individuals. Finally, **refinement** involves improving procedures and techniques to minimize pain and stress for animals. Almost all animal care guidelines apply only to vertebrates, with one notable exception: in the United Kingdom, animal care guidelines cover cephalopods.

Governmental, research, and educational facilities that receive US federal funding are required to have their research monitored by an institutional animal care and use committee (IACUC). Before conducting research on animals, each scientist must submit an animal care protocol to the committee, which is composed of institutional scientists, a veterinarian, and members of the outside community. The protocol must describe why a species is appropriate for the research and whether nonanimal alternatives are available. For example, is it possible to use recordings from previous work? Could computer modeling replace live animals? The protocol must also justify the number of individuals required, how they will be procured, and specific conditions for animal care (e.g., housing enclosure, food provided, temperature, and light/dark regime). In addition, the scientist must describe procedures that will be used to minimize stress to the animals and address what will be done with them after the study is completed. Can they be used for future research? Will animals be released back into the wild at their capture sites, or will they be euthanized?

The IACUC reviews the research protocol to make sure that all animals will receive appropriate care and that the research is well designed, has not been conducted before, and complies with all animal welfare regulations. The committee also assesses the importance of the research question and the quality of the research before allowing it to be conducted. As you can see, ethical considerations are an important factor in animal behavior research. Next, we examine how scientists communicate their research findings to the scientific community.

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## 2.4 Scientific knowledge is generated and communicated to the scientific community via peer-reviewed research

### Learning Objectives

After reading this section, you should be able to

- describe the peer-review process,
- analyze a publication to determine if it had been peer-reviewed, and
- explain why peer review is an important aspect of scientific knowledge.

Every day we hear about important scientific discoveries in areas ranging from human health to the environment. How do we evaluate all this information? How do we determine what is based on valid research and what is just personal opinion? The ability to evaluate scientific information critically and ascertain its validity is called scientific literacy. However, scientific literacy would not be possible if scientists could not evaluate and communicate their research in the first place. Even the most far-reaching discoveries remain unknown until scientists communicate their findings to the world.

Animal behavior research is conducted by investigators and their graduate and undergraduate students at universities, zoological parks, veterinary schools, government and private research institutions, and conservation organizations. After conducting research, scientists write papers and submit them to scientific journals to report their findings. These journals, known as the **primary literature**, are the primary, or original, source of scientific

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information (**Figure 2.12**). The editors of scientific journals use experts to help decide whether to accept or reject a paper for publication, a process known as **peer review**. Reviewers evaluate the importance of the research question and the validity of the hypotheses, methodology, analyses, and conclusions. They also comment on how clearly and concisely the paper is written; if a paper is poorly written, it will be difficult for the reader to evaluate the science. Reviewers scrutinize manuscripts for accuracy, and papers are rejected for such reasons as unsound methodology, incorrect analyses or statistics, poor experimental design, and faulty or inappropriate logic. As a result, the knowledge communicated in the primary literature has passed a rigorous, objective review.



**FIGURE 2.12.** Scientific journal. *Behavioral Ecology* is a peer-reviewed journal devoted to animal behavior research.

Scientific papers typically follow a systematic format of a title, abstract, methods, results, and discussion with conclusions (see **Toolbox 2.2**). For instance, the methods section contains detailed information about how the research was conducted. Such an explanation is important because other scientists must be able to replicate the work in order to test its validity. The paper may also contain figures and tables that summarize important findings. Most natural scientists follow the style manual of the Council of Science Editors (CSE), which describes how to cite references and handle other matters of style. Psychologists and other social scientists follow the American Psychological Association (APA) format, while medical journals tend to use that of the American Medical Association (AMA). Here we follow a modified version of the author-year system of the CSE style (e.g., [Nordell & Valone 1998](#)).

### TOOLBOX 2.2

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## Scientific literacy

When we hear or read about a scientific discovery, we tend to assume that the information is an accurate and unbiased representation of the original finding. To evaluate the accuracy of the report, it is important to be able to refer to the primary literature. How can you determine whether the information you are reading is peer reviewed (from the primary literature), an interpretation of the research (from the secondary literature), or simply someone's personal opinion? Answering this question is an important part of scientific literacy and is critical to being an informed citizen. This information can affect our health, the environment, and how we vote. Here are some key questions to ask.

1. **What is the name of the publication, and is it endorsed by a scientific society?**

Show Answer

2. **Who are the authors?**

Show Answer

3. **Is the article written in the standard scientific format, with an introduction, a methods section, a results section, a discussion or conclusion, and literature cited or references list?**

Show Answer

4. **Does the article cite the primary literature in the references?**

Show Answer

5. **Does the publication indicate that all articles are peer-reviewed?**

Show Answer

If the results of scientific research are of interest to the public, they may also be reported in newspapers, magazines, and books, as well as on television and the internet. Reports like these are called the **secondary literature** because the information has been presented before and often does not have the same validity as the primary literature ([Toolbox 2.2](#)).

Peer review is a hallmark of most research. It allows experts in a field to evaluate potential new knowledge critically. However, hypothesis testing remains the domain of the sciences and provides a means for the rapid advancement of our knowledge about the natural world.

## CHAPTER SUMMARY AND BEYOND

Animal behavior researchers generate and test hypotheses. Hypotheses can be developed through observations or the use of analytical models. To test hypotheses, researchers commonly use observational, experimental, and comparative methods. The observational method is least invasive to the animal and provides data both to describe behavior and to test hypotheses. In the experimental method, researchers manipulate variables to determine their effect on behavior, providing insight into how specific factors affect behavior. The comparative method examines similarities and differences among closely related species to infer patterns of evolutionary change in a trait.

In all research that involves animals, it is imperative to minimize individuals' stress and suffering. Research on animals is monitored and must be approved by institutional (and sometimes federal) animal care and use committees. The three Rs—replacement, reduction, and refinement—are often used as guidelines. Researchers must consider the possibility of replacing animals with computer models, reducing the number of animals required, and refining their techniques to minimize stress and disturbance to the animals used. For a more complete treatment of this subject, see [Armstrong and Botzler \(2016\)](#), [Dawkins \(2008\)](#), and [Allen and Bekoff \(2007\)](#).

Scientific literacy is the ability to evaluate scientific information critically. It includes understanding how hypothesis testing drives the scientific process, as well as peer review, in which scientists determine whether research is clear, valid, and important enough to be published in the primary literature. [Laine and Mulrow \(2003\)](#) describe the value of peer review and provide insights into how the process works. [Elisabeth Pain \(2016\)](#) provides a useful overview of the review process from multiple perspectives. Papers in scientific journals follow a consistent, systematic format. The public often reads about these research studies in the secondary literature.



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# CHAPTER 1

## The Science of Animal Behavior

Shawn E Nordell  
Washington University in St. Louis

Thomas J Valone  
Saint Louis University

### Concepts

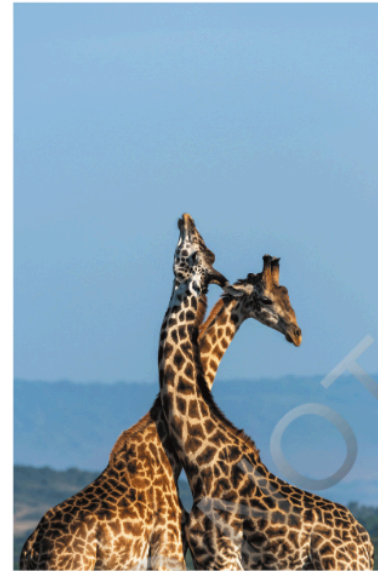
- 1.1 [Animals and their behavior are an integral part of human society](#)
- 1.2 [The scientific method is a formalized way of knowing about the natural world](#)
- 1.3 [Scientists study both the proximate mechanisms that generate behavior and the ultimate reasons why the behavior evolved](#)
- 1.4 [Researchers have examined animal behavior from a variety of perspectives over time](#)
- 1.5 [Anthropomorphic explanations of behavior assign human emotions to animals and can be difficult to test](#)

### Features

- |                               |   |
|-------------------------------|---|
| <b>Scientific Process</b>     | 1.1 <a href="#">Robin abundance and food availability</a>     |
|                               | 1.2 <a href="#">Robin abundance and predators</a>             |
| <b>Applying the Concepts</b>  | 1.1 <a href="#">Human infant crying</a>                       |
|                               | 1.2 <a href="#">What is behind the "guilty look" in dogs?</a> |
| <b>Toolbox</b>                | 1.1 <a href="#">Describing and summarizing data</a>           |
|                               | 1.2 <a href="#">Interpreting graphical data</a>               |
| <b>Quantitative Reasoning</b> | 1.1 <a href="#">Nesting success and breeding habitats</a>     |

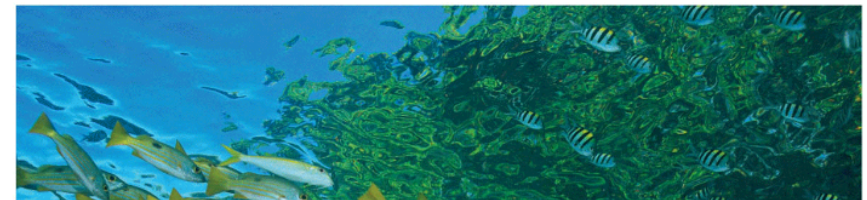
We can observe animal behavior everywhere. Millions of people enjoy bird-watching, both in their yards and around the world. Squirrels are also easily observed in many urban and suburban environments and exhibit a variety of interesting behaviors, such as chirping and wagging their tails when a predator is nearby. Each spring,

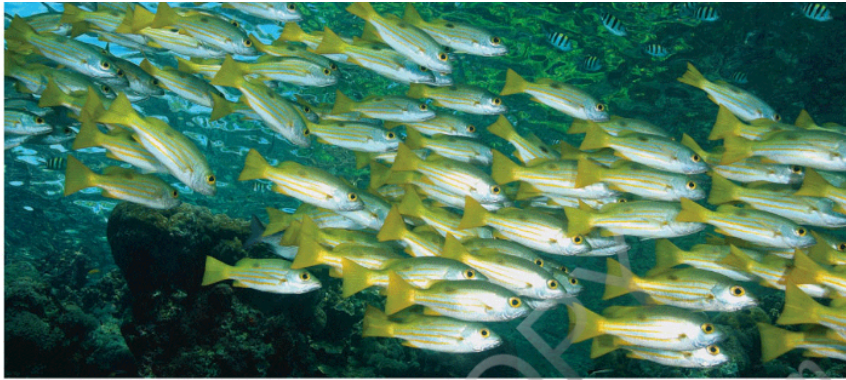
frogs, crickets, and cicadas can be heard singing to attract mates while wasps can be seen making nests under eaves of houses, where the queen lays eggs and workers care for offspring. Farther from our home male giraffes in Africa exchange blows by swinging their heads and necks against one another in competition for females ([Figure 1.1](#)), while fish in the Great Barrier Reef form large schools to minimize predation ([Figure 1.2](#)).



**FIGURE 1.1.** Giraffe behavior. An aggressive interaction between two males.

This book will introduce you to the wonders of animal behavior. In this chapter, we begin by exploring the ways that animals and their behaviors are an important part of the world. We then introduce the science of animal behavior and the scientific method. We'll see how scientists test hypotheses to learn about the natural world and examine a fundamental characteristic of animal behavior research: it looks at both the proximate mechanisms that generate that behavior as well as the ultimate reasons for why it evolved. We'll examine the varied approaches and perspectives used to study animal behavior. Finally, we discuss that although most scientific hypotheses about behavior are developed in the context of evolution, many nonscientists try to explain animal behavior based on the idea that animals possess human emotions.





**FIGURE 1.2.** Schooling fish. Snapper form schools to minimize predation.

#### Video: Two male giraffes perform necking behavior

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reasons for why it evolved. We'll examine the varied approaches and perspectives used to study animal behavior. Finally, we discuss that although most scientific hypotheses about behavior are developed in the context of evolution, many nonscientists try to explain animal behavior based on the idea that animals possess human emotions.



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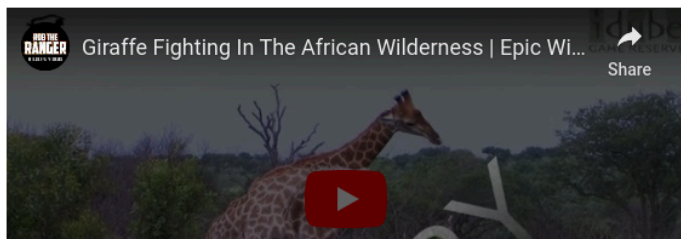
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## 1.1 Animals and their behavior are an integral part of human society

### Learning Objectives

After reading this section, you should be able to

- describe several ways that humans and animals interact,
- recognize and describe animal behavior, and
- explain what an ethogram is and how it is created.

Understanding the behavior of animals has always been important to people. Beginning in prehistoric times and continuing for tens of thousands of years, humans painted images of animals on cave walls all over the world. These drawings are detailed enough that we can identify different species (both extinct and extant), and many images depict animals exhibiting behaviors such as eating, sleeping, and engaging in acts of aggression. Recent research indicates that these paintings were likely intended to present realistic depictions of animals and their behavior rather than to evoke symbolic connotations (Pruvost et al. 2011). Because humans in prehistoric times relied on animals for food, knowledge about animal behavior was important for survival (Shipman 2010).

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Animals and animal behavior are still an integral part of society. Millions of people live and interact with animals daily. The American Veterinary Medical Association reports that in 2011, in the United States alone, over 80 million households contained a pet (American Veterinary Medical Association 2012). This number includes 139 million freshwater fish, 90 million cats, 73 million dogs, 18 million other small mammals, 16 million birds, and 11 million reptiles. Most owners value their pets for companionship: we enjoy both watching our pets behave and interacting with them.

Many people work with animals. Cattle, chickens and turkeys, hogs, and sheep are important livestock; horses are used in ranching, sports, and law enforcement; and dogs have long been used in both police work and the military (e.g., Ensminger 2012) (Figure 1.3). In all these cases, people manage animal behavior to accomplish a task. In a different way, the behavior of animals is also integral to medicine; it helps researchers assess and learn about sensory, motor, and cognitive functions. For instance, behavioral changes often reflect the effects of neurochemical agents, neurotoxins, or hormonal changes, which can be more easily studied in animals than in humans. Research on memory, cognitive function, and learning often involves measuring and recording animal behavior.



**FIGURE 1.3. Police working dogs.** Dogs are used as trackers and substance detectors.

In addition, animals provide entertainment for millions of people. According to the World Association of Zoos and Aquariums, more than 700 million people visit zoos and aquariums worldwide each year (Gusset & Dick 2011). Many movies and popular television shows feature animal behavior, and entire television networks, such as Animal Planet and National Geographic Wild, are dedicated to animals.

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Yet the study of animal behavior involves much more than interacting with pets, working with animals, or watching animals in movies or on television. Animal behavior researchers use the scientific method to understand the behaviors we observe. So what exactly do we mean by *behavior*?

### Video: Military dog training

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## Recognizing and defining behavior

We define **animal behavior** as any internally coordinated, externally visible pattern of activity that responds to changing external or internal conditions (Beck, Liem, & Simpson 1991; Levitis, Lidicker, & Freund 2009). Let's examine each part of this definition in turn.

*Internally coordinated* refers to internal information processing such as endocrine signaling, sensory information processing, or the action of neurotransmitters. When two male giraffes meet during the breeding season, such processes coordinate their aggressive behavior. However, when the wind blows through a lion's mane, the animal is *not* exhibiting a behavior; it has no control over this movement.

*Externally visible activity* refers to patterns that we can observe and measure. For example, we can observe a squirrel eating an acorn and can quantify this behavior. We cannot externally observe the variation in a lizard's heart rate.

We can, however, observe an animal's *behavioral response to changing conditions*. For example, male crickets, frogs, and birds vocalize in response to changes in day length, temperature, or moisture at specific times of the year. Similarly, during a summer day, a desert lizard moves from the top of a hot rock to the underside of a cool ledge to reduce its body temperature (Figure 1.4). Lizards are *ectotherms*; as such, they can regulate their body temperature behaviorally but not internally.



**FIGURE 1.4. Lizard thermoregulation.** Ectotherms, like this chuckwalla (*Sauromalus varius*), move to cool locations as their body temperature rises.

FEATURED RESEARCH **Measuring behavior in elephant ethograms**

Behaviors must be measurable—that is, we must be able to quantify our observations with numbers according to specific rules (Martin & Bateson 1993)—and different people must be able to recognize a behavior independently. Often, such characterization begins when a trained observer completes an **ethogram**, which is a formal description or inventory of an animal’s behaviors. Ethograms typically list or catalogue defined, discrete behaviors that a particular species exhibits. Researchers can use an ethogram to record how many times a behavior occurs (its frequency), the length of time of a behavior (its duration), the

We turn next to a discussion of the scientific method: the process scientists use to understand the behaviors they observe.

**Video: Elevated hay feeders mimic natural feeding behaviors**

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**1.2 The scientific method is a formalized way of knowing about the natural world**

## Learning Objectives

After reading this section, you should be able to

- apply the scientific method to evaluate the validity of a claim;
- evaluate positive and negative results in relation to a tested hypothesis, and provide valid conclusions;
- explain the relationship between correlation and causality; and
- differentiate between a hypothesis and a theory.

When you think of science, you may think first of an impressive body of knowledge—the facts that you are asked to learn in class. Have you ever considered where that knowledge came from? It was obtained by human beings seeking to understand the natural world. Scientists engage in the **process of science**, which involves observing events, organizing knowledge, and providing testable explanations (Mayr 1982). The process of science is fundamental to our understanding of the natural world.

Scientific discoveries continue to occur at a tremendous pace. Every week, new discoveries appear on television, in magazines, and on the internet. As instructors, we look back at our courses from just five years ago and marvel at how much has changed in so short a time. You and your instructors may be involved in new discoveries yourselves. Why does scientific progress occur so rapidly? What is different about scientific knowledge compared with knowledge in the humanities? As we see next, the process of science means constructing hypotheses that make testable predictions.

## The importance of hypotheses

In every discipline, scholars seek to gain a better understanding of the world. Researchers in the humanities, which includes English, history, and philosophy, are interested in understanding the human experience. The social sciences, like anthropology and sociology, involve knowledge of human behavior and societies. And in the natural sciences, such as biology and chemistry, researchers strive to understand the natural world.

You may have noticed differences between your courses not only in the information presented but also in how you are expected to think about that information. For example, the humanities discuss art, literature, and how humans think and act. You might be expected to present your own perspective while critically evaluating the perspectives of others. Often, two people may arrive at very different perspectives using similar evidence.

Historians, for example, strive to understand why certain events happened by interpreting personal journals, letters, government publications, and newspaper articles. A historian forms a thesis, or narrative, to explain events and then interprets relevant documents to support that thesis (Hult 2002). For instance, a historian might be interested in what motivated American founding fathers to declare independence from England and form their

own system of government. Were economic considerations, such as preservation of individual wealth, the primary motive (Beard 1913), or did convictions about individual liberty and rights play a larger role (McDonald 1958)? By examining the Declaration of Independence, the US Constitution, the *Federalist Papers*, and letters written by key figures, historians have developed these and other interpretations. In each case, research involves discovering, reevaluating, and interpreting the evidence.

Scientists, like other scholars, begin with questions, which they formulate into hypotheses. You may think of a hypothesis as an educated guess, but this definition is far too simplistic. A research **hypothesis** is an explanation that is based on assumptions and produces a testable prediction. Because these tests can be repeated and confirmed by other scientists, their results are much less subject to debate. This is why science sometimes seems like just an accumulation of facts. Yet these facts are the results of scientific studies that have been confirmed repeatedly by the scientific community over many years.

## The scientific method

The scientific method is a formalized process that involves testing hypotheses (Figure 1.6). This process often begins with an observation of a single event or pattern that requires explanation and thus forms the basis of a **research question**—a brief statement of something that we would like to understand. Suppose you were walking through your neighborhood and observed that some yards had many American robins (*Turdus migratorius*) feeding in them, while other yards had very few. Robins, common songbirds found on lawns throughout North America, feed on invertebrates such as earthworms and beetle grubs. Your observation might lead to the following research question (Scientific Process 1.1):

**Research question:** Why is there variation in the number of robins feeding in different yards?

### SCIENTIFIC PROCESS 1.1

#### Robin abundance and food availability







Research Question: *Why is there variation in the number of robins feeding in yards?*

### Hypothesis:

The amount of food in a yard determines the number of robins feeding there.

### Prediction:

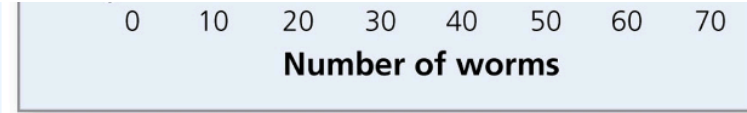
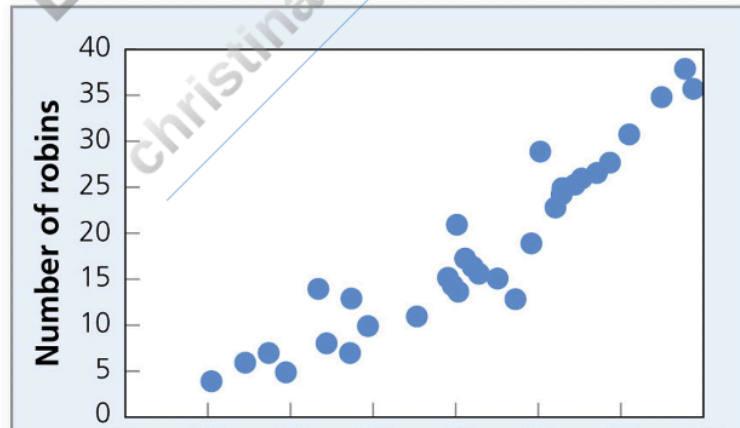
Yards with more food will have more robins.

### Methods:

The researchers:

- Counted the number of robins at the same time of day in each of 30 yards
- Quantified the amount of food (earthworms) available to robins in each yard by examining several 900 cm<sup>2</sup> sampling areas
- Mixed 40 g of yellow ground mustard seed into 4 L of water and then poured the mixture into each sampling area so that it was absorbed into the soil
- Counted the number of earthworms that emerged in each sampling area over a period of ten minutes

### Results:

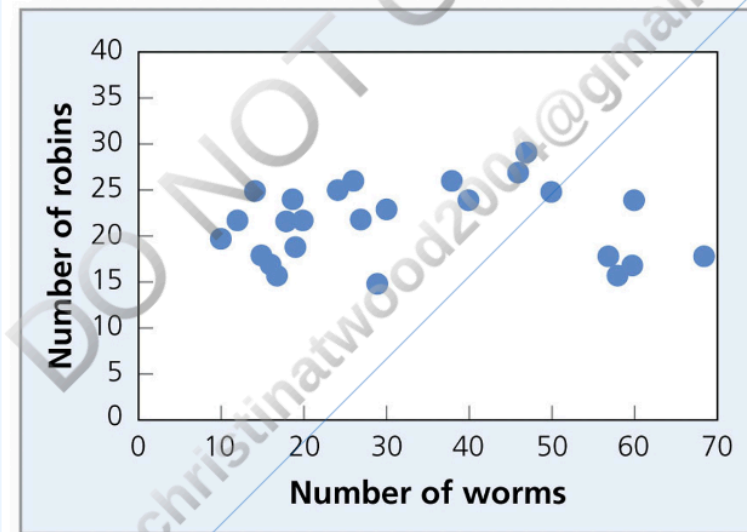


**FIGURE 1.** The greatest numbers of robins were found in yards with the most worms.

### Conclusion 1:

The hypothesis is supported. Yards with more earthworms have more robins.

OR



**FIGURE 2.** There is no relationship between the number of robins and the number of worms in yards.

### Conclusion 2:

The hypothesis is not supported. Yards with more earthworms do not have more robins.

## Evaluate

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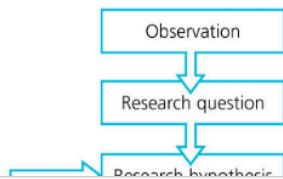
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The identification of such patterns can be accomplished with careful observation and mere human curiosity. Throughout this book, you will see how researchers have identified different behavioral patterns that have led to a variety of research questions.



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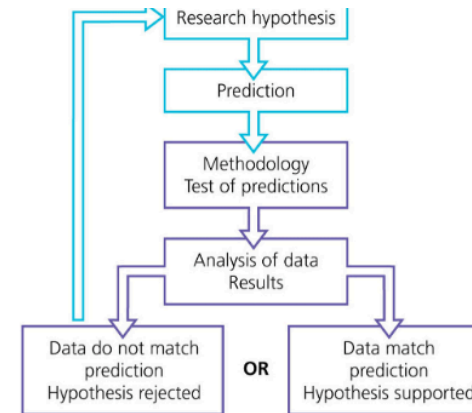


FIGURE 1.6. The scientific method. This flowchart summarizes the scientific method.

The next step in the scientific process is the formulation of a hypothesis, or, more formally, a research hypothesis. Research hypotheses are evaluated using two statistical hypotheses that reflect the two possible outcomes. One is that the proposed explanation for the observation *does* have a significant effect; this is the **alternate hypothesis, or  $H_a$** . The other is that the proposed explanation does *not* have a significant effect; this is the **null hypothesis, or  $H_0$** , the hypothesis of no effect. These terms were coined by Sir [Ronald Fisher \(1966\)](#) a British geneticist, evolutionary biologist, and statistician.

Let's return to our example. To explain why more robins feed in some yards than in others, you might hypothesize that the quantity of food varies between yards and that this variation affects robin abundance. This leads to two statistical hypotheses:

**Alternate hypothesis:** The amount of food in a yard determines the number of robins feeding there.

**Null hypothesis:** The amount of food in a yard does not determine the number of robins feeding there.

The alternate hypothesis assumes that the amount of food in a yard is the only factor that determines the number of robins feeding there. Both the alternate and null hypotheses make predictions, although they are different:

**Alternate hypothesis prediction:** Yards with more food will have more robins.

**Null hypothesis prediction:** There is no relationship between the amount of food in a yard and the number of robins in the yard.

The last step in the scientific process is to evaluate the research hypothesis by testing the prediction of the null hypothesis. One way to do this is to make new observations by collecting and analyzing data from many different yards on

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on a smoker's intention to quit, quitting success rate, and so forth. Alternatively, social scientists could conduct an experiment. Smokers might be randomly assigned to receive either antismoking educational material or a fictional article (as a control). Again, the researchers would collect data on each smoker's intention to quit, quitting success rate, and so forth. Many other factors might also affect tobacco use, such as income or social factors, and these too would need to be considered.

Where does the study of animal behavior fall in this framework? Animal behavior courses are typically offered by biology or psychology departments. Animals are a part of the natural world, and so it makes sense that animal behavior is a part of the natural sciences. Why, then, is it also studied in psychology departments? The answer is that psychologists have two ways to study human behavior: (1) directly or (2) indirectly, through the study of animals, in the same way that medicine uses animal models to understand human health. Psychological research on the evolution of human behavior often involves the study of our closest relatives. Animal behavior research, whether conducted by biologists or psychologists, uses the scientific method to formulate and test hypotheses.

### 1.3 Scientists study both the proximate mechanisms that generate behavior and the ultimate reasons why the behavior evolved

#### Learning Objectives

After reading this section, you should be able to

- describe Tinbergen's four questions and provide examples of each and
- explain the significance of Tinbergen's work in animal behavior.

What kinds of research questions can we ask about animal behavior? Consider that many birds travel long distances between summer breeding and winter nonreproductive grounds. We can ask several questions about this migration behavior—for example, “What initiates such movements?” Migratory behavior often is initiated by seasonal changes in day length, which trigger hormonal responses that lead to increased feeding, fat deposition, and the onset of long-distance movement ([Ramenofsky & Wingfield 2007](#)). Another question is, “How does migratory behavior develop in individuals?” In some species, migration behavior is genetically determined and so requires no learning. In others, migration routes must be learned by following experienced individuals (e.g., [Lishman et al. 1997](#)) ([Figure 1.8](#)).



**FIGURE 1.8. Migration.** Sandhill cranes (*Grus canadensis*) learn migration routes by following experienced individuals.

We can also ask, “Why do birds migrate?” Migration allows individuals to track resources and thus avoid places where resource availability is greatly limited in particular seasons; in short, migration behavior promotes survival ([Cox 1985](#)). Finally, “How did migration behavior evolve in a species or within a group of related species?” To understand how this evolved, researchers often examine how migration patterns differ among various populations of a species or between closely related species ([Outlaw et al. 2003](#)).

#### Tinbergen's four questions

The Dutch biologist and ornithologist [Niko Tinbergen \(1963\)](#) articulated four basic questions that can be asked about animal behavior:





1. What is the mechanism that causes the behavior?
2. How does the behavior develop?
3. How does the behavior affect survival and reproduction?
4. How did the behavior evolve?

Tinbergen's four questions provide a framework for the study of behavior. Answers to Questions 1 and 2 are often referred to as **proximate explanations** because they focus on underlying mechanisms of a behavior such as physiological, genetic, neurosensory, and cognitive mechanisms, including learning ([Mayr 1961](#)). Answers to Questions 3 and 4 are known as **ultimate explanations** because they require evolutionary reasoning and analysis. [Tinbergen \(1963\)](#) argued that a complete understanding of behavior requires answers to all four questions ([Applying the Concepts 1.1](#)). Note that the two kinds of explanations involve different time scales (current behavior versus its development or history) ([Table 1.2](#)).

**TABLE 1.2 Tinbergen's four questions.** Proximate and ultimate questions and answers regarding birdsong.



TABLE 1.2 Tinbergen's four questions. Proximate and ultimate questions and answers regarding birdsong.

	Focus on Current State	Focus on History
Proximate Explanations	<p>Q1: What mechanism causes the behavior to occur?</p> <p>A1: Changes in seasonality trigger hormonal responses that initiate song production.</p> 	<p>Q2: How does the behavior develop in the individual?</p> <p>A2: Young birds often learn song from adults.</p> 
Ultimate Explanations	<p>Q3: How does the behavior affect survival and reproduction?</p> <p>A3: Birdsong can function to attract mates.</p> 	<p>Q4: How did the behavior evolve?</p> <p>A4: Birdsong variation depends upon evolutionary history.</p> 

(Source: Adapted from Nesse [2013] and Kokko [2017])

## APPLYING THE CONCEPTS 1.1

### Human infant crying

We can adopt [Tinbergen's \(1963\)](#) approach to more fully understand not only animal but also human behaviors. For example, Debra Zeifman summarized over 100 studies on human infant crying from the perspective of Tinbergen's four questions ([Zeifman 2001](#)):

1. What is the mechanism that causes the behavior?

Show Answer

2. How does the behavior develop?

Show Answer

3. What is the function of the behavior?

Show Answer

4. How did the behavior evolve?

Show Answer

## Implications of Tinbergen's work

Tinbergen's work had a major impact on research in animal behavior. In particular, he inspired research on ultimate explanations, which had previously been under-studied ([Taborsky 2014](#)). One lasting effect of his work is the emphasis on proximate and ultimate explanations as complementary rather than alternative. Both types of explanation provide fuller insight into observed behavior. Indeed, many animal behavior scientists ask proximate and ultimate questions in their research.

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## 1.4 Researchers have examined animal behavior from a variety of perspectives over time

### Learning Objectives

After reading this section, you should be able to

- explain comparative psychology, and differentiate the work of Thorndike and Lloyd Morgan from that of Romanes;
- distinguish how the approaches used by behaviorists differ from those used by classical ethologists; and
- identify the three classical ethologists who shared the 1973 Nobel Prize in Physiology and Medicine, and describe their important contributions to animal behavior.

From Darwin forward, animal behavior research has been based on evolutionary thinking. However, during this time a large number of rich and diverse research foci have placed different emphases on Tinbergen's four questions and have developed varied approaches and methodologies. In this section, we briefly review how animal behavior research has changed over time.

### Darwin and adaptation

Darwin pioneered the scientific study of behavioral adaptation in three books: *On the Origin of Species* (1859), *The Descent of Man and Selection in Relation to Sex* (1871), and *The Expression of the Emotions in Man and Animals* (1872). In the first book, Darwin discusses instinct, or behaviors neither learned nor requiring experience. One intriguing example he describes is cuckoo reproductive behavior. Many species of cuckoo lay their eggs in the nests of other species, which then care for the young (Figure 1.9). How could such behavior evolve by natural selection? Darwin notes that, while most female birds lay an egg every day, female cuckoos lay one every several days. He reasons that, if a female cuckoo were to raise her own eggs, she would be faced with a prolonged period of incubation and a clutch of chicks with widely varying ages. Such a scenario would be costly for both the female

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of incubation and a clutch of chicks with widely varying ages. Such a scenario would be costly for both the female and the chicks. Darwin hypothesizes that selection would favor an individual that laid her eggs in the nests of others, circumventing this problem.



**FIGURE 1.9. Cuckoo behavioral adaptation.** A common redstart (*Phoenicurus phoenicurus*) feeds a larger cuckoo chick. Many species of cuckoo lay their eggs in the nests of other species.

Darwin's work on animal behavior is wide ranging, both taxonomically (e.g., ants, birds, and bees) and topically (e.g., reproduction, aggression, and instinct). Although some of his descriptions are based on anecdotes and others are anthropomorphic, Darwin always explains behavior using evolutionary reasoning and in terms of adaptation. His work represents the beginning of the evolutionary basis of animal behavior research, a tradition that has continued through to today.

### Early comparative psychology

George Romanes, a contemporary of Darwin, approached the study of animal behavior from the perspective of a comparative psychologist. Psychologists study the mental processes and behavior of humans. Comparative psychologists, like Romanes, study animal behavior in order to understand human behavior. In *Animal Intelligence*, Romanes systematically examines the reasoning ability of a wide variety of animal taxa, ranging from protozoans to mammals (Romanes 1882). For him, an animal displays a "mind," or conscious action, rather than mere reflex reaction, when it uses previous experiences to learn and modify its behavior in an adaptive manner. For example, if a protozoan encounters a barrier and moves around it, Romanes interprets this behavior as evidence of a conscious or intelligent choice, as opposed to a reflex movement.

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Romanes's work stimulated other researchers to focus on examining animal consciousness. He eventually published a "mental tree" to describe a hierarchy of reasoning among taxa ([Romanes 1888](#)). While this construction is simplistic, the patterns it summarizes are surprisingly congruent with current research regarding which animals display higher stages of cognitive development. These include tool use in monkeys and communication in Hymenoptera, one of the largest orders of insects ([Burghardt 1985](#)).

Many of the examples in Romanes's book are anecdotal or anthropomorphic, and they were often provided by nonscientists. So although it was one of the first attempts to systematically examine behavior throughout the animal kingdom, it was heavily criticized. For instance, C. Lloyd Morgan emphasized the need

#### Interdisciplinary approaches

Psychologists and ethologists have conducted animal behavior research increasingly as an interdisciplinary endeavor over the last few decades. For instance, we've seen the development of evolutionary psychology and cognitive ethology, disciplines that both emphasize the study of animal thought processes and cognition using an evolutionary framework. Evolutionary psychologists seek to understand human thinking and behavior, while cognitive ethologists focus on understanding the behavior of animals and often integrate information from neuroscience. Both fields assume that natural selection has shaped brain architecture and thought processes in an adaptive manner. Evolutionary psychologists, such as John Tooby and Leda Cosmides, suggest that we can best explain human behavior by understanding how natural selection shaped neural mechanisms in the past ([Griffiths 2008](#)).

Cognitive ethologists also seek to understand how natural selection has acted on mental processes and cognition in order to better understand the behavior of animals. In doing so, they often conduct comparative studies using broad taxonomic comparisons, frequently carrying out research in natural environments. Donald Griffin is credited with the development of cognitive ethology thanks to his book *The Question of Animal Awareness* ([Griffin 1976](#)). Today, cognitive ethologists study topics such as learning and memory, counting ability, symbol recognition, and vocal communication in organisms as diverse as bees, crows, rodents, and primates ([Bekoff, Allen, & Burghardt 2002](#)).

Behavioral ecology, which developed in the 1960s and 1970s and continues today, focuses on the evolution of behavior by studying its function. As such, the focus of behavioral ecology is on understanding the adaptive value of behavior. Behavioral ecology research often begins with theory (either mathematical or computer models) to examine the fitness benefits and costs of different behaviors. These models are used to predict the behavior that maximizes fitness; these predictions are then tested empirically. What behavioral ecologists learn from this process helps us understand how natural selection has molded behavior ([Davies, Krebs, & West 2012](#)).

You can already see that various perspectives place different emphases on Tinbergen's four questions. For example, classical ethologists tend to focus on proximate questions, while behavioral ecologists often emphasize ultimate explanations of behavior. Throughout this book you will read examples of both proximate and ultimate research studies.

## 1.5 Anthropomorphic explanations of behavior assign human emotions to animals and can be difficult to test

### Learning Objectives

After reading this section, you should be able to

- define anthropomorphism and provide an example and



- explain why anthropomorphism is problematic in the study of animal behavior.

**Anthropomorphism** is the tendency to attribute human motivations, characteristics, or emotions to animals. For example, a documentary might describe a female coyote (*Canis latrans*) as “worried” when her mate is late returning to the den and as “happy” when he returns with food. Another show might describe a female meerkat (*Suricata suricatta*) as “sad” when her grown offspring leave the den to establish their own territories. Of course, many cartoons depict animals as essentially humans in animal form—talking, singing, showing feelings, and scheming to achieve different goals.

Perhaps because anthropomorphism is so prevalent in the media, it is also very common among the public ([Applying the Concepts 1.2](#)). People often attempt to explain the behavior of animals by attributing their actions to anger, envy, or shame. For example, imagine that a bee stung your leg as you tried to swat it away. Using anthropomorphic thinking, you might believe that the bee stung you because you made it angry. This explanation may or may not be true, but how could you possibly test it? What prediction does this explanation make? It is difficult, if not impossible, to characterize the emotional state of a bee.

## APPLYING THE CONCEPTS 1.2

### What is behind the “guilty look” in dogs?

Have you ever come home to find food missing off the counter or the garbage strewn all over the floor? Many dog owners have experienced this and have immediately scolded their dog for disobedience. They often report that their dogs display a “guilty look” because they “know” they have been disobedient ([Figure 1](#)). These owners describe this look as avoiding eye contact, lying down and rolling on the side or back, wagging the tail low and quickly, holding the head down, licking or pawing, and/or moving away from the owner. But do dogs experience “guilt”? This is an anthropomorphic explanation of a behavior.



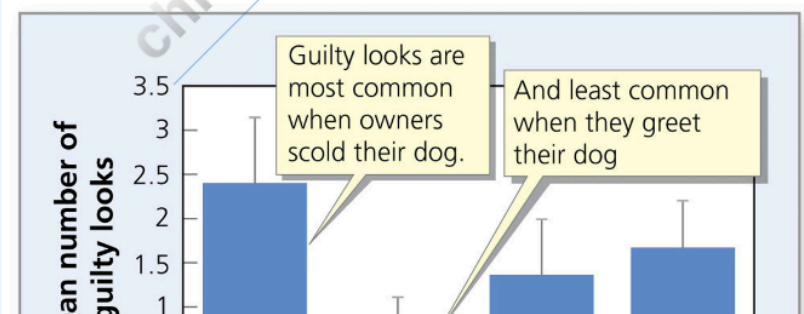
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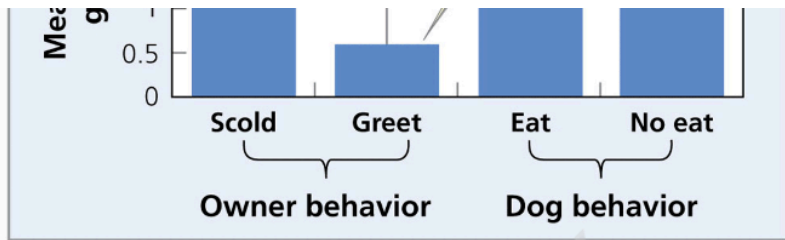
**FIGURE 1.** Guilty look.

Alexandra Horowitz, a cognitive scientist who studies dog behavior, designed an experiment to examine the guilty look in 14 dogs ([Horowitz 2009](#)). Each dog was exposed to four experimental treatments. At the beginning of each trial, the owner showed the dog a treat, told the dog not to eat it, and left the room. The experiment had two conditions: either (1) the researchers gave the dog the treat (the dog ate the treat and disobeyed the owner's command) or (2) the researchers removed the treat (the dog could not eat the treat or disobey the owner's command). Once the treat was gone, the owners were called back into the room. They were told either that (1) the dog ate the treat or (2) the dog did not eat the treat (it had been removed), although this information may or may not have been true. Each dog experienced all pairwise combinations of the conditions. Owners were instructed to scold their dogs when told the treat had been eaten and to greet their dogs in a friendly manner when told the treat had not been eaten. All trials were videotaped, and the researchers quantified the number of times each dog displayed the aforementioned behaviors associated with the guilty look.

Horowitz found that the dog's obedience had no effect on its display of guilty look behaviors: the mean number of guilty look behaviors was similar whether or not the dog actually ate the treat. Owner behavior did affect dog behavior, however, because guilty look behaviors were most common after owners scolded their dogs (although in half of these trials, the dog had not disobeyed the command) and least common when they greeted their dogs ([Figure 2](#)). Horowitz concluded that the dogs did not display more behaviors associated with the guilty look after disobeying a command. She speculates that the guilty look likely represents submissive behavior in response to owner scolding. But she notes that her experiment does not rule out the possibility that dogs could experience guilt. Anthropomorphic explanations of animal behavior remain intriguing but difficult to test. ■



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**FIGURE 2.** Dog responses. The mean (+ SE) number of guilty looks was highest when dogs were scolded by their owners. (Source: Horowitz 2009)

One hypothesis to explain the bee's behavior does make a prediction: the bee perceived your attempt to swat it as an attack, leading to antipredator behavior. In other words, bees sting potential predators to deter attacks. You could test this hypothesis by observing interactions between bees and their predators and then quantifying how often individuals use their stingers. As a control group, you could compare the interactions between bees and a nonpredator and quantify how often bees sting that species. The hypothesis would predict that bees will more often sting potential predators than they will nonpredators.

While anthropomorphic thinking rarely produces testable predictions, we do not want to dismiss the possibility that animals experience emotions. Understanding animal thinking is challenging, but researchers are making progress in its study, as we will see in [Chapter 7](#). In addition, for many animals, there is often a relationship between stress-related behaviors and physiology, as with the production of glucocorticoid steroids in vertebrates ([Blas et al. 2007](#)). In these cases, we are making progress in understanding animal mental states and emotions. However, anthropomorphic hypotheses remain a challenge to test and we should be cautious using such explanations unless we have compelling evidence supporting them.

## TOOLBOX 1.2

### Interpreting graphical data

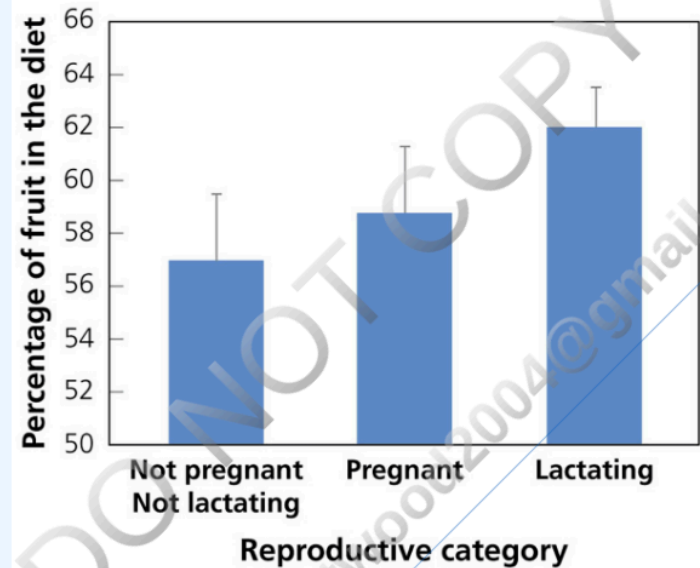
Scientists use graphs as visual representations of their data. Graphs allow us to observe trends or relationships between variables, differences between groups, and relative proportions in data. Understanding and interpreting graphs includes quantitative skills of reading the data, qualitative skills of reading between the data, and analytical skills of reading beyond the data. We will discuss each of these as we deconstruct the different types of commonly used graphs.

### Graph Standards and Types of Graphs

The type of graph used will depend on the type of data and the relationship being displayed between the variables. Each axis of the graph should have a label. All graphs should have a succinct, descriptive title and a caption that summarizes the major point(s) of the graph. If there

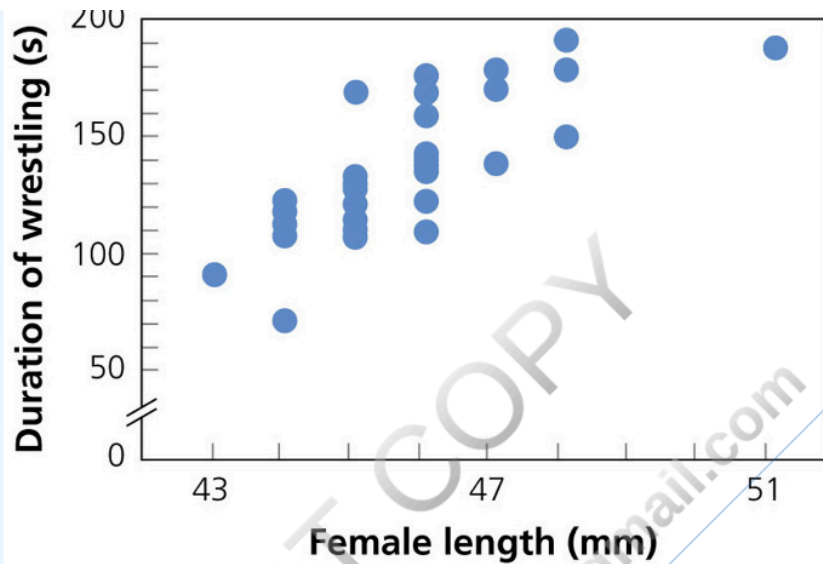
are multiple series or bars, a legend may be included to identify each grouping of data points. In this Toolbox, we discuss each type of commonly used graph used in this textbook.

**Bar graphs** ([Figure 1](#)) are used to represent categorical data in which the x axis shows the categories and the y axis represents their values, with the height or length of the bar being proportional to the value of each category. Bar graphs display data in discrete categories such as males and females, different populations, mating sites, or diets, as well as control and treatment individuals.



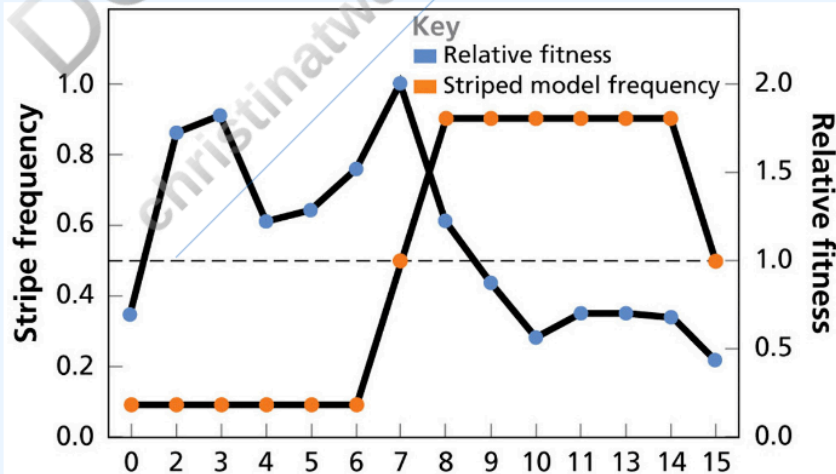
**FIGURE 1.** Bar graph—Chimpanzee diet. Mean (+ SE) percentage of fruit in the diets of females with different reproductive conditions. Pregnant and lactating females ate more fruit than nonpregnant, nonlactating females. (Source: Murray et al. 2009)

**Scatter plots** display the relationship between two measured variables such as running speed and limb length, or the amount of time spent foraging and the amount of food consumed. Each data point represents the value of both the x and y variables. Examples of scatter plots are regressions and correlations. In regressions, the independent variable is the x axis because it is something that we can measure, control, or manipulate. The dependent variable is the y axis and measures the response to changes in the independent variable. The regression line shows the pattern of relationship between the two variables. For correlations, there is no dependent or independent variable because the correlation simply displays the patterns of association between the two variables. [Figure 2](#) is an example of a correlation.



**FIGURE 2.** Scatter plot—Duration of wrestling in male red-spotted newts. The duration of wrestling increased with the size of the female that was amplexed. (Source: Verrell 1986)

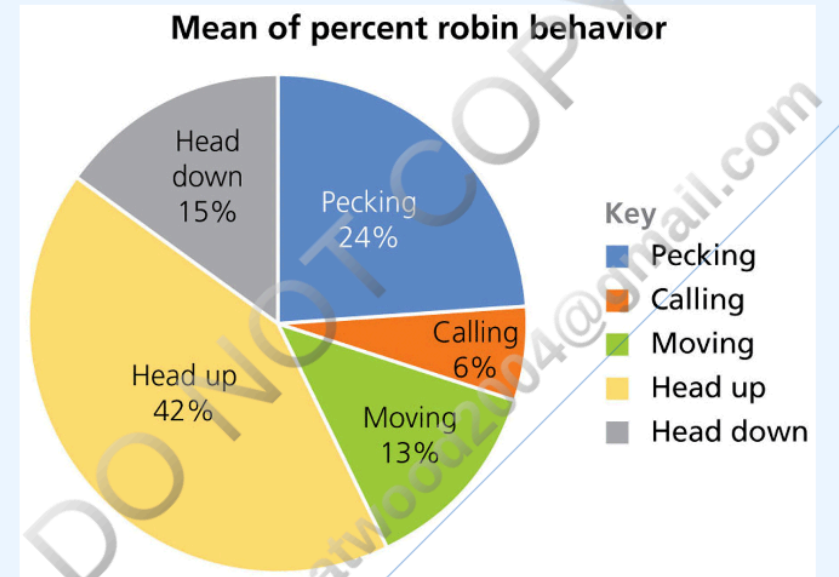
**Line charts, or line graphs** (Figure 3), are similar to a scatter plot, but data points are ordered on one or both axes and the points are connected by lines. This allows generalized trends to be displayed.



## Day

**FIGURE 3.** Line chart—Frequency and fitness. The daily frequency of striped models (orange) and their relative fitness (blue). (Source: Fitzpatrick, Shook, & Izally 2009)

**Pie charts** (Figure 4) summarize data in a circle with different sectors representing different categories in the data. The size of each sector represents the categories' proportional amount of the data.



**FIGURE 4.** Pie chart—Time budget of robin behaviors. The mean daily percentage of time spent in different behaviors.



## CHAPTER SUMMARY AND BEYOND

Animal behavior is important because it intersects with the lives of many people. We define behavior as the internally coordinated activity patterns of animals that respond to changing external or internal conditions. [Levitis, Lidicker, and Freund \(2009\)](#) provide a useful review of the many definitions of behavior that scientists use. Modern animal behavior research involves more than simply observing animals; it also involves testing hypotheses to explain behavior.

Science is a way of knowing about the natural world by using the scientific method. Scientists use the scientific method to construct hypotheses that make testable predictions. Researchers analyze data to determine whether they support or refute their hypothesis. Science never proves a hypothesis is correct—it is an ongoing process of hypothesis testing, and that process is crucial to scientific progress. A hypothesis that makes broad predictions and stands up to repeated testing may eventually become a theory. Scientists must consider the limitations of studies that report correlations because correlation does not demonstrate causation.

Explanations about animal behavior address either proximate or ultimate research questions, as summarized by [Tinbergen \(1963\)](#). While researchers' emphasis on proximate and ultimate explanations has varied, together these explanations provide complementary information and a more complete understanding of behavior. [Laland et al. \(2011\)](#) examine contemporary biological debates in light of the proximate–ultimate dichotomy.

Beginning with Darwin, researchers have studied behavior from many perspectives. [Houck and Drickamer \(1996\)](#) offer a detailed description of the history of the study of animal behavior, including seminal papers. [Dewsbury \(1985\)](#) provides autobiographies of many important figures in the history of animal behavior research.

Finally, anthropomorphic hypotheses assign human emotions to animals; they are difficult to test but are an area of active discussion ([Bekoff and Pierce 2009](#)). For a review of the history and problems associated with anthropomorphism in the scientific study of animal behavior, see [Wynne \(2004; 2007\)](#).

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## Chapter Summary and Beyond

Animal behavior is important because it intersects with the lives of many people. We define behavior as the internally coordinated activity patterns of animals that respond to changing external or internal conditions. [Levitis, Lidicker, and Freund \(2009\)](#) provide a useful review of the many definitions of behavior that scientists use. Modern animal behavior research involves more than simply observing animals; it also involves testing hypotheses to explain behavior.

Science is a way of knowing about the natural world by using the scientific method. Scientists use the scientific method to construct hypotheses that make testable predictions. Researchers analyze data to determine whether they support or refute their hypothesis. Science never proves a hypothesis is correct—it is an ongoing process of hypothesis testing, and that process is crucial to scientific progress. A hypothesis that makes broad predictions and stands up to repeated testing may eventually become a theory. Scientists must consider the limitations of studies that report correlations because correlation does not demonstrate causation.

Explanations about animal behavior address either proximate or ultimate research questions, as summarized by [Tinbergen \(1963\)](#). While researchers' emphasis on proximate and ultimate explanations has varied, together these explanations provide complementary information and a more complete understanding of behavior. [Laland et al. \(2011\)](#) examine contemporary biological debates in light of the proximate–ultimate dichotomy.

Beginning with Darwin, researchers have studied behavior from many perspectives. [Houck and Drickamer \(1996\)](#) offer a detailed description of the history of the study of animal behavior, including seminal papers. [Dewsbury \(1985\)](#) provides autobiographies of many important figures in the history of animal behavior research.

Finally, anthropomorphic hypotheses assign human emotions to animals; they are difficult to test but are an area of active discussion ([Bekoff and Pierce 2009](#)). For a review of the history and problems associated with anthropomorphism in the scientific study of animal behavior, see [Wynne \(2004; 2007\)](#).